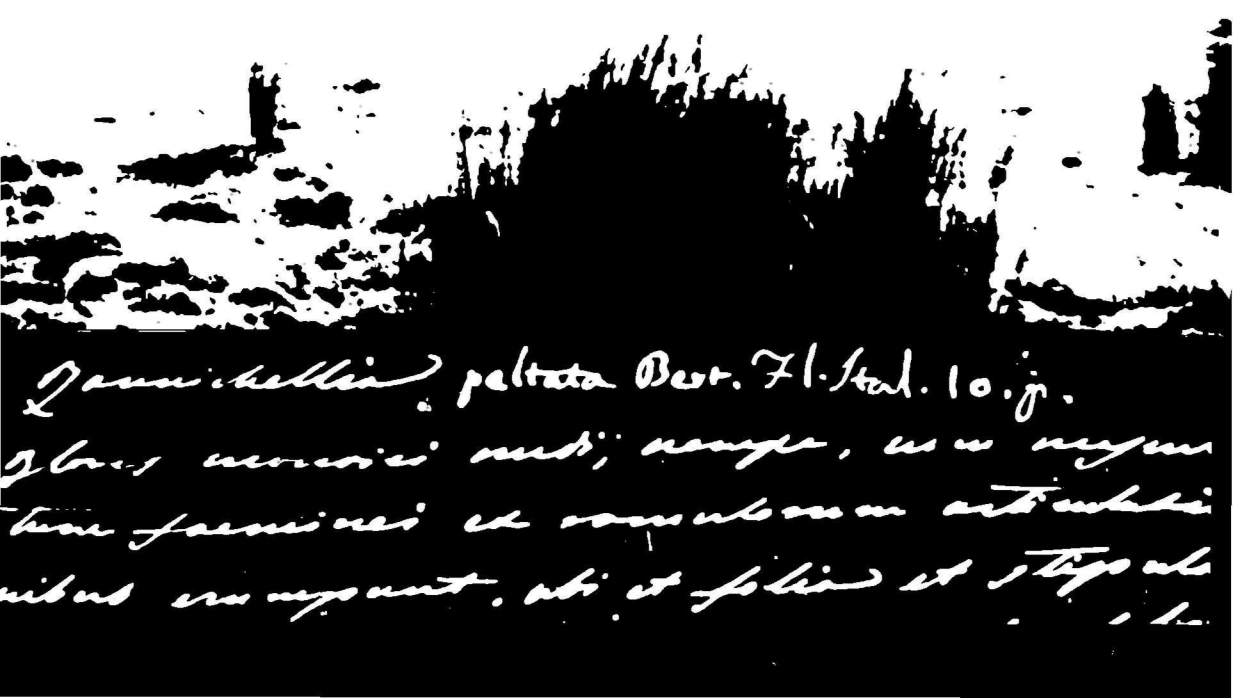
THE ECOLOGY OF COMMUNITIES DOMINATED BY *ZANNICHELLIA* TAXA IN WESTERN EUROPE

W. van Vierssen



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Promotor: Prof. Dr. C. den Hartog

THE ECOLOGY OF COMMUNITIES DOMINATED BY *ZANNICHELLIA* TAXA IN WESTERN EUROPE

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IN DE WISKUNDE EN NATUURWETENSCHAPPEN
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1982
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en Frank
Aan Anke

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I am very indebted to all graduate students of the University of Nijmegen, who participated in the *Zannichellia* project during the period 1976-1980. I would also like to thank all the biologists from the University of Helsinki (Finland), the "Institut für Seenforschung und Fischereiwesen" at Reichenau (W.Germany), the "Station Biologique de la Tour du Valat", Camargue (France), the University of Sevilla (Spain) and the "Estacion Biologica de Doñana" (Spain) for their discussions and assistance.
I am also very grateful for financial support from the Beyerinck-Popping Fund and the Ministry of Health and Environmental Protection.

Rhenen, February 1982,
Wim van Vierssen.

The ecology of communities dominated by *Zannichellia* taxa in western Europe

CONTENTS

Aquatic Botany, 12 (1982) 103—155
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THE ECOLOGY OF COMMUNITIES DOMINATED BY *ZANNICHELLIA* TAXA IN WESTERN EUROPE. I. CHARACTERIZATION AND AUTECOLOGY OF THE *ZANNICHELLIA* TAXA

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ABSTRACT

Van Vierssen, W., 1982. The ecology of communities dominated by *Zannichellia* taxa in western Europe. I. Characterization and autecology of the *Zannichellia* taxa. *Aquat. Bot.*, 12: 103—155.

On the basis of *Zannichellia* material collected in Finland, Denmark, The Netherlands, W. Germany and France, three species could be distinguished: *Z. palustris* L., *Z. pedunculata* Rchb. and *Z. major* Boenn. A fourth species, *Z. peltata* Bertol., was found in southern Europe. A table with identification characteristics for these four *Zannichellia* species is given. *Z. palustris* usually has $2n=24$ chromosomes, whereas *Z. pedunculata* has $2n=36$ chromosomes. *Z. peltata* is discussed in relation to the tetra- and hexaploid taxa.

The germination ecology of *Z. palustris* and *Z. pedunculata* was extensively studied. By means of the harmonic mean germination day (HMGD) -index, germination was studied in relation to chlorinity, temperature and desiccation under long-day conditions and in the dark. The dormancy of all *Z. palustris* seeds was remarkable. It could be broken by a stratification period of 2 months (4°C). After stratification the seeds germinated under long-day conditions in water with a salinity up to $4‰$ Cl'. *Z. pedunculata* seeds germinated extremely well only in the light. After stratification germination also occurred in the dark and the optimum temperatures for germination were lower under various chlorinity conditions, with the lowest optimum temperature in the dark. The seeds germinated in water with a chlorinity up to $12‰$ and were not damaged by desiccation lasting several months.

Z. major seeds germinated without delay. A survey of the germination capacity of the seeds of these *Zannichellia* taxa from several European localities is presented. Selected plants of both *Z. palustris* and *Z. pedunculata* developed best on substrates with a relatively high clay content. The chlorinity tolerances of the two species did not differ to a large extent. *Z. palustris* showed a maximum chlorinity tolerance of about $8‰$, and *Z. pedunculata* of about $10‰$.

Z. pedunculata produced a relatively low number of long shoots while *Z. palustris* produced numerous small shoots. This difference in shoot production was advantageous to *Z. pedunculata* in mixed populations under conditions of fluctuating (rising) chlorinity.

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SCOPE OF THE RESEARCH PROJECT

This study is part of a research project, dealing with the structure and function of communities dominated by aquatic macrophytes, which was started in 1973 by the Department of Aquatic Ecology in Nijmegen, The Netherlands. Within this project, data have already been obtained with respect to structural aspects, faunistic and floristic composition, and productivity of communities dominated, respectively, by *Ruppia* spp. (Verhoeven, 1975, 1978, 1979, 1980a, 1980b, Verhoeven and van Vierssen, 1978a, 1978b), by *Zostera* spp. (Jacobs, 1979) and by Nymphaeids, with emphasis on *Nymphoides peltata* (Gmel.) O. Kuntze (van der Velde, 1979, 1980; van der Velde et al., 1979, van der Velde and Brock, 1980, van der Velde and van der Heijden, 1980).

This part of the research project concerns communities dominated by *Zannichellia* taxa (and a number of accompanying aquatic macrophytes of the genus *Potamogeton*) in western Europe. These communities can to a certain extent be regarded as transitional between the *Ruppia*-dominated communities in poikilohaline waters and the more differentiated true freshwater communities.

This study was started in the summer of 1976. In view of existing taxonomical problems much attention was paid to the variation in morphological characteristics and the distinction of taxa. Several countries in Europe were visited, viz. Finland, Denmark, Germany and France, to collect plant material and to investigate the communities. Most attention was paid to the communities in The Netherlands. The results will be published in three parts.

Part I deals with the distinction and description of the west European *Zannichellia* taxa. The germination ecology of these has been studied extensively. The influence of factors such as chlorinity, temperature, light conditions, stratification and desiccation upon the germination capacity and germination rate has been established. The growth-form and biomass of *Zannichellia* taxa have been studied in relation to environmental factors such as chlorinity and sediment composition by means of experiments. To explain different distribution patterns in nature, competition experiments with some of the *Zannichellia* taxa have been performed under controlled conditions

Part II contains the results of the field studies. The distribution of the taxa is given in relation to environmental factors (salinity, substrate and water depth). The life cycles of the different taxa in nature are described in relation to geographical latitude, field conditions and the results of the autecological experiments dealt with in Part I. The species composition of the macrofauna, inhabiting the phytal zone dominated by *Zannichellia* taxa, is discussed and a classification of the communities is given, based on the qualitative composition of the macroflora and macrofauna.

Part III deals with the chemical ecology of the communities in The Netherlands. The chemical composition of the different macrophyte species is unravelled by means of comparative studies of plant tissue concentrations (N, P,

Ca, Mg, Mn, Fe, K, Na). The nutrient content of *Zannichellia* plant tissue has been studied in relation to nutrient content of the substrate. Concentrations in separate plant parts have been studied and relationships between underground and aboveground plant parts have been mathematically expressed. By means of cluster analysis, similarities between sampling stations (water analysis and sediment analysis) and of plant species have been calculated. Finally, nutrient pools such as the sediment, water, seston and aquatic macrophytes were studied in a selected *Zannichellia* dominated community during one growing season, in order to elaborate an approximate nutrient budget.

INTRODUCTION

Z. palustris s.l. is a widely distributed taxon found in freshwater as well as in coastal and inland saline waters, in mountain areas as well as at sea level. The most elaborate studies with respect to taxonomy and ecology of the genus have been conducted in western Europe (Luther, 1947, 1951a, 1951b; Reese, 1963, 1967). Outside Europe, the genus *Zannichellia* is treated as monospecific. *Z. palustris* s.l. is said to occupy a very wide range of habitats and a correspondingly large amount of material had to be collected to trace relevant morphological and ecological characteristics. To exclude habitat-induced differences, much *Zannichellia* material from different European localities has been cultured under controlled conditions. The disagreement among authors with respect to the taxonomic position of the different taxa is striking. A taxon called a species by one author is found as a subspecies or a variety in other studies. This study, however, is not a taxonomical one, and therefore no taxonomical revision is presented. The nomenclature is also of a provisional character. Most of the basic information with respect to the *Zannichellia* taxa distinguished in the various parts of western Europe was found in Luther (1947) and Reese (1963, 1967). In the west European material a number of well defined *Zannichellia* taxa can be recognized by their morphological characteristics. The autecological characteristics of these taxa are also studied.

MORPHOLOGICAL CHARACTERIZATION OF THE WEST EUROPEAN *ZANNICHELLIA* TAXA

A problem in the study of the ecology of the different *Zannichellia* taxa is the very difficult interpretation of morphological characteristics in different European areas. A comparison of the identification keys of several authors reveals no clear characteristics that are valid in the whole of western Europe.

TABLE I

Identification characteristics of *Zannichellia* species in western Europe

Distinguishing characteristics		
A Length of mature stamen > 3 cm		
B. Length of mature stamen ≤ 3 cm	a. Length of mature fruit > 3.0 mm	
	b. Length of mature fruit < 3.0 mm	
	1. $\frac{\text{Length of rostrum}}{\text{Length of fruit}} < 0.50$	
	Fruit length 1.82—2.54 mm	
	2. $\frac{\text{Length of rostrum}}{\text{Length of fruit}} \geqslant 0.50$	
	Fruit length 2.25—2.80 mm	

In this section, various morphological characteristics are dealt with and their range determined from material collected in several localities (Fig. 1). On the basis of this material, a table with identification characteristics for the west European *Zannichellia* taxa is given (Table I).

Additional characteristics

Chromosome number 2n=12 — *Zannichellia peltata* Bertol

Denmark 3.15 mm
Finland 3.40 mm

Number of fruits Denmark 2—(4)—8
Finland 2—6 } 2—8

Leaf-width 1.0—2.0 mm
Chromosome number 2n=32 — *Zannichellia major* Boenn.

The Netherlands 0.37—0.40
W. Germany 0 38—0.39
Denmark 0.30—0.35
Finland 0.22—0.30 } 0.22—0.40

Leaf-width in running waters, often up to 1.0 mm; in stagnant waters, 0.3—0.5 mm
Number of fruits W. Germany 2—(3—4—5)—10
The Netherlands 2—(3—4)—5
Denmark 2—(2)—4
Finland 2—(4)—6 } 2—10
Chromosome number 2n=24 — *Zannichellia palustris* L. —

a. mature fruits with smooth convex side, very fine general morphology with small shoots spp. *repens* (Boenn.) Koch

b. mature fruits with very irregularly shaped convex side, relatively robust general morphology with long shoots spp. *palustris*

France 0.55—0.58
The Netherlands 0.60—0.79
Denmark 0.53—0.70
Finland 0.50 } 0.50—0.79

Leaf-width 0.3—1.5 mm
Number of fruits France 2—(3)—5
The Netherlands 1—(4)—6
Denmark 1—(4)—5
Finland (2)—3 } 1—6
Chromosome number 2n=36 — *Zannichellia pedunculata* Rchb.

Morphology of fruits and seeds

A very important characteristic in the identification of the different *Zannichellia* taxa has always been the morphology and number of fruits. In Fig. 2A and B, the different parts of the fruit-body used as characteristics in the identification are indicated. *Z. major* could be separated from the other material collected in Europe because the size of the fruits exceeds that found

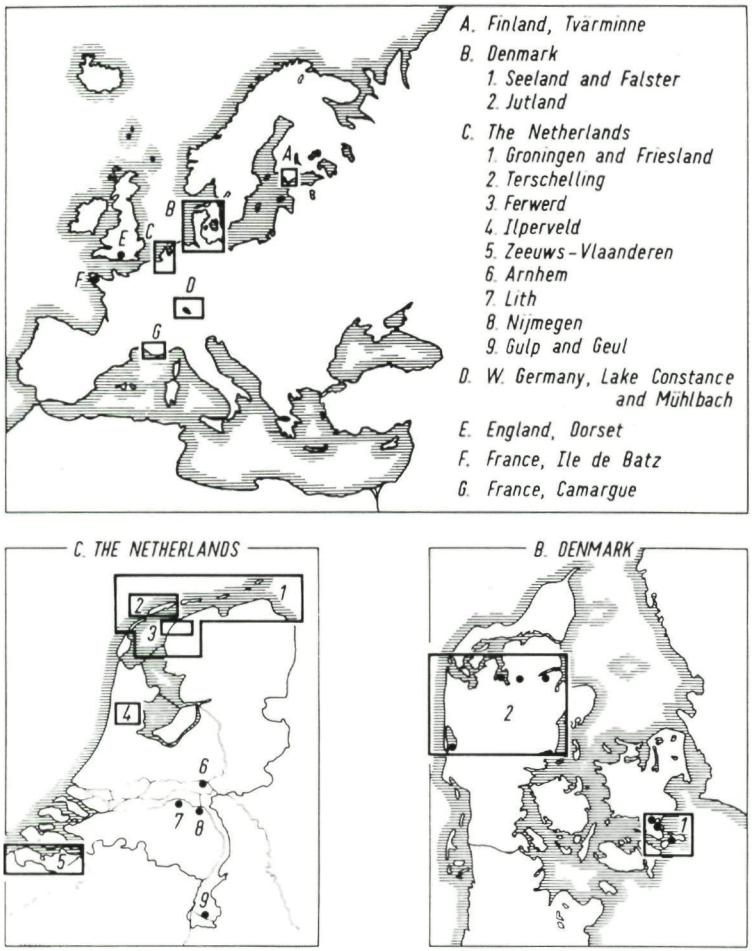


Fig. 1. Distribution of the major sampling areas in western Europe.

in the other *Zannichellia* taxa. In Fig. 2A it can be seen that the mean fruit length of *Z. palustris* is less (2.24±0.23 mm) than the mean fruit length of *Z. pedunculata* (2.62±0.18 mm). *Z. major* fruits reach a mean length of 3.4 mm. As can be seen, fruits of *Z. palustris* collected in Lith (The Netherlands) are bigger than fruits of *Z. pedunculata* collected in Tvärminne (Finland). So, the validity of this morphological criterion in the distinction of these two taxa is restricted to material from the same area. From Fig. 2A it is obvious that the rostrum length plays an important role in the distinction. The mean rostrum length of the *Z. palustris* fruits is 0.78±0.20 mm and of *Z. pedunculata* 1.69± 0.29 mm. Fruits of *Z. palustris* originating from the river Geul (The Netherlands) show a rostrum length which approximates that of fruits of *Z. pedunculata* from Tvärminne (Finland). When comparing the rostra of

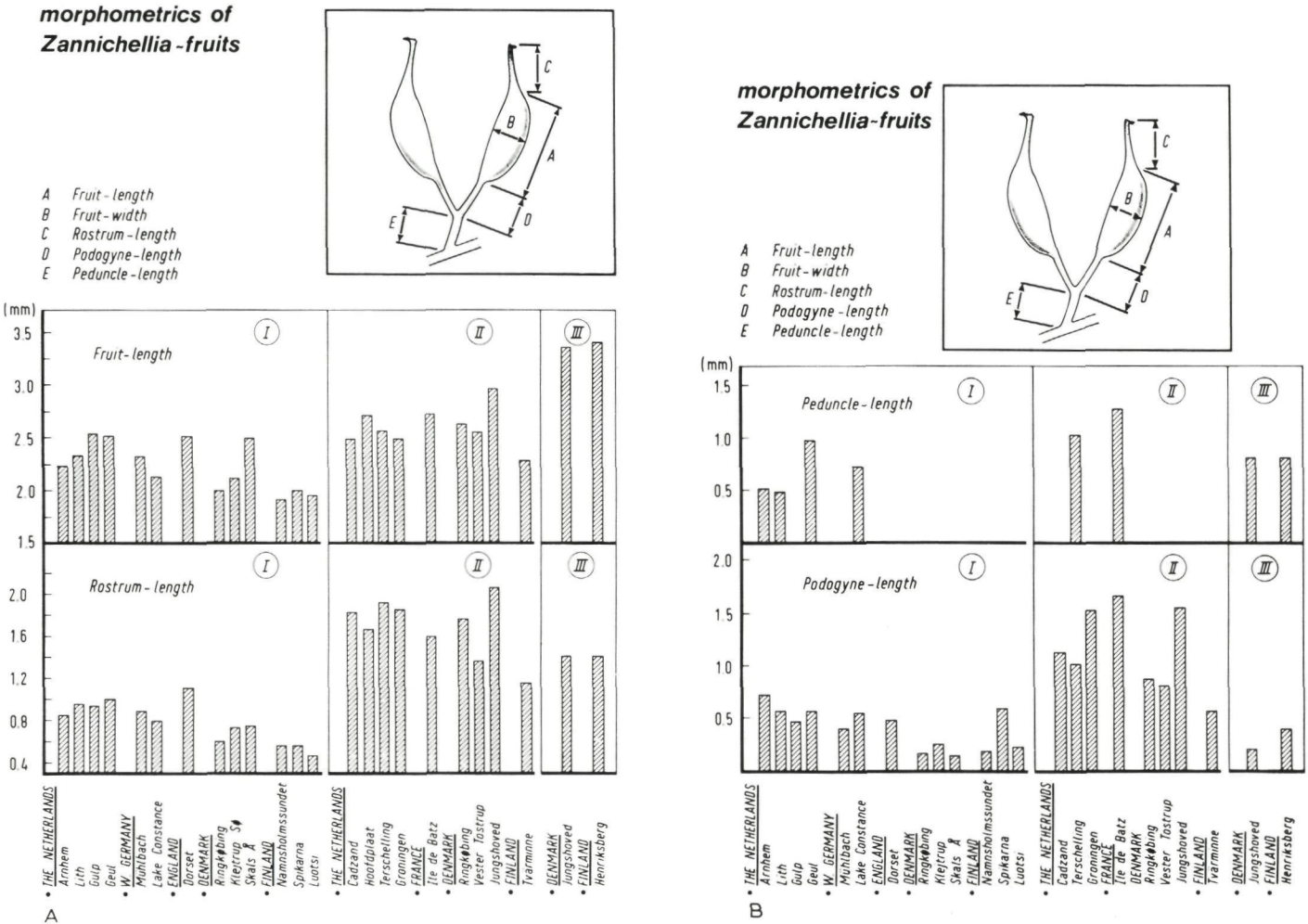


Fig. 2. Morphometrics of *Zannichellia* fruits. I, *Z. palustris* L.; II, *Z. pedunculata* Rchb.; III, *Z. major* Boenn.

fruits from the same area, those of *Z. palustris* are shorter than those of *Z. pedunculata*. The podogyne lengths (Fig. 2B) show considerable differences when comparing the taxa. The mean length is 0.40±0.19 mm in *Z. palustris* and 1.13±0.40 mm in *Z. pedunculata*. The very small podogyne length of *Z. major* is striking considering the fruit length. These large and robust fruits are apparently subsessile. Relatively few data were collected with respect to the peduncle length. As Reese (1967) pointed out with respect to *Zannichellia* material from Germany, the rostrum/fruit length ratio is an important characteristic in the distinction between *Z. palustris* (sub nomine *Z. palustris* L. ssp. *palustris*) and *Z. pedunculata* (sub nomine *Z. palustris* ssp. *pedicellata* Rosén & Wahlenb.). *Z. palustris* and *Z. pedunculata* could be separated by means of this ratio as is illustrated in Fig. 3.

In Fig. 4A and B some scanning electron micrographs (SEM) are given which reveal certain structures and characteristics with respect to seeds from the different taxa. The pericarp has slowly decayed and the seeds (as they are called after the decay and discarding of the pericarp) reveal a general morphology which can be largely different in detail when compared with the fruit morphology. From Fig. 4A (b, d, f) it is obvious that in the same

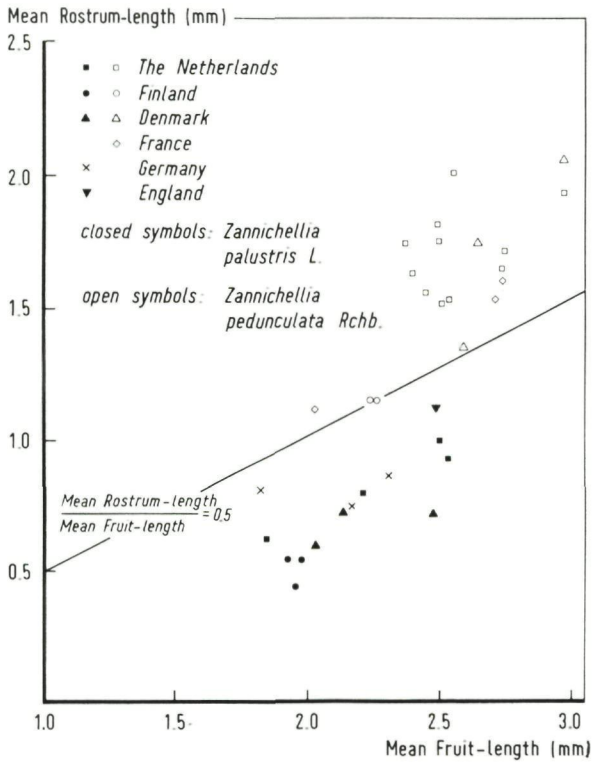
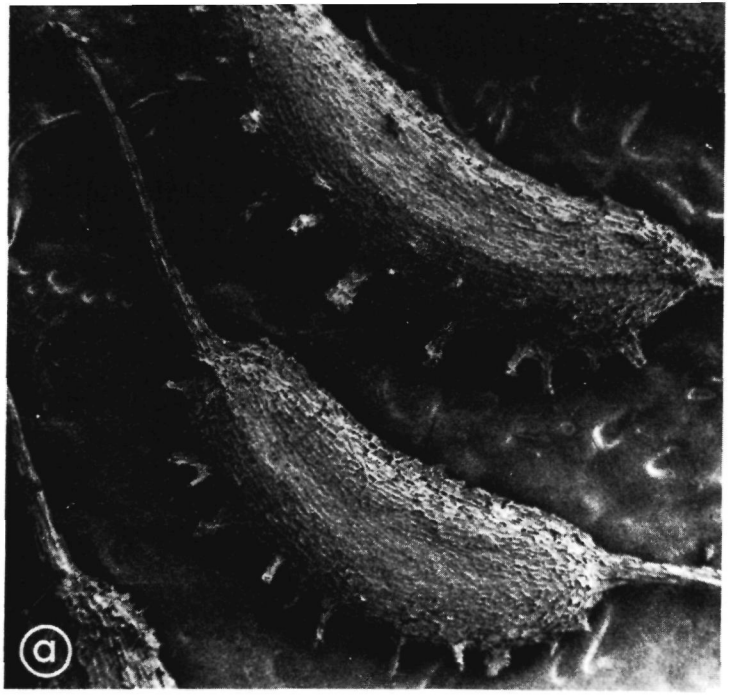


Fig. 3. The distinction of *Z. palustris* L. and *Z. pedunculata* Rchb. according to the mean rostrum/mean fruit-length ratio.



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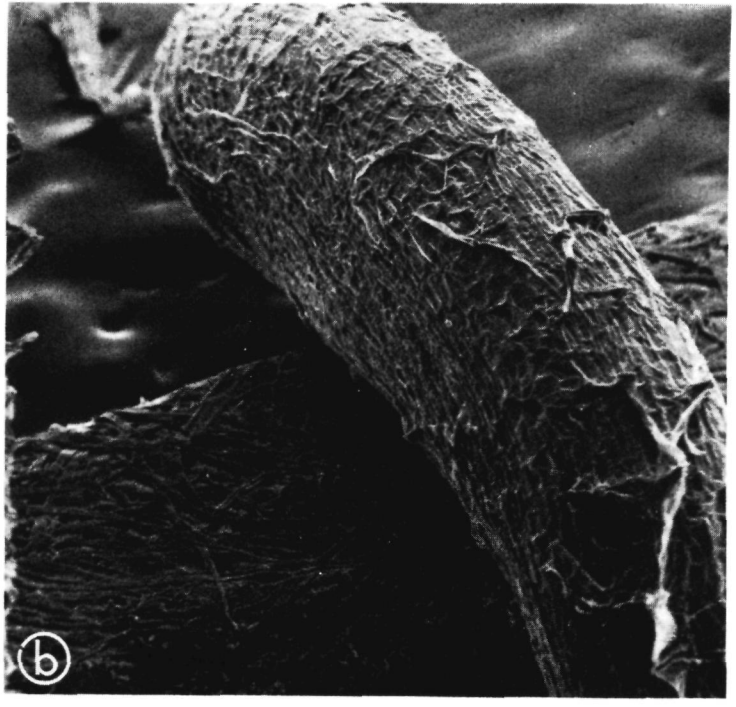
DENMARK



LITH,
THE NETHERLANDS

Fig. 4. Electron scanning micrographs of ripe seeds from different localities in western Europe: (A) a, e, *Z. pedunculata* Rchb.; b, c, d, f, *Z. palustris* L. (B) a, b, *Z. palustris* L.; c, d, *Z. pedunculata* Rchb.; e, f, *Z. major* Boenn.

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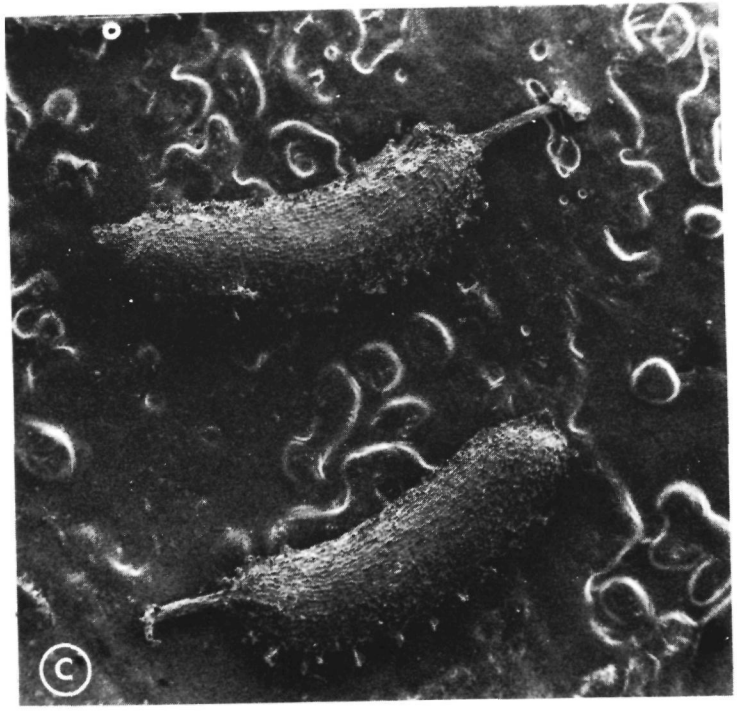

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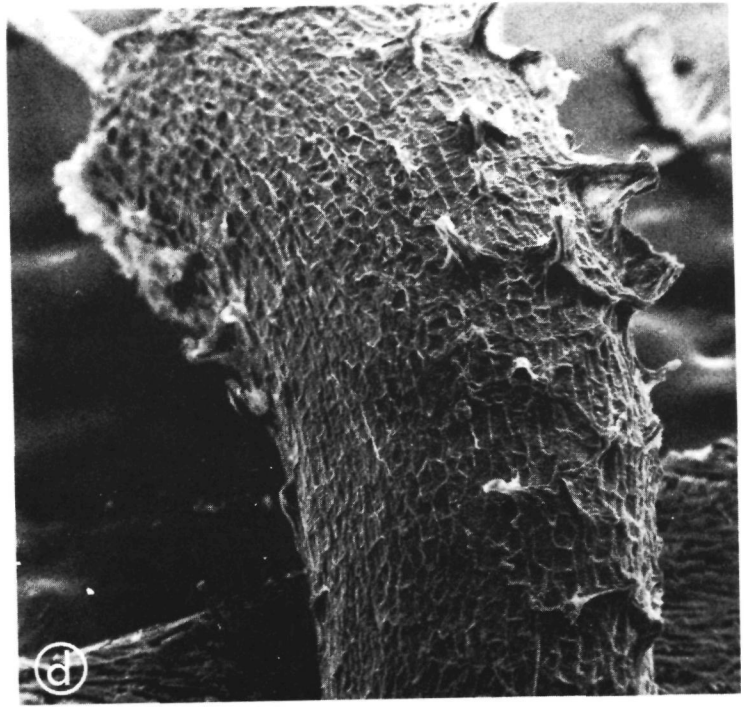
DENMARK



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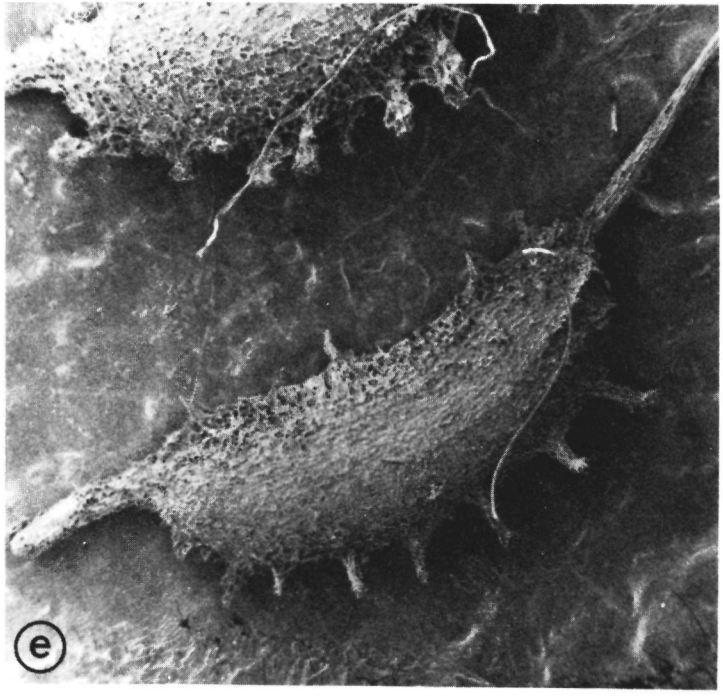
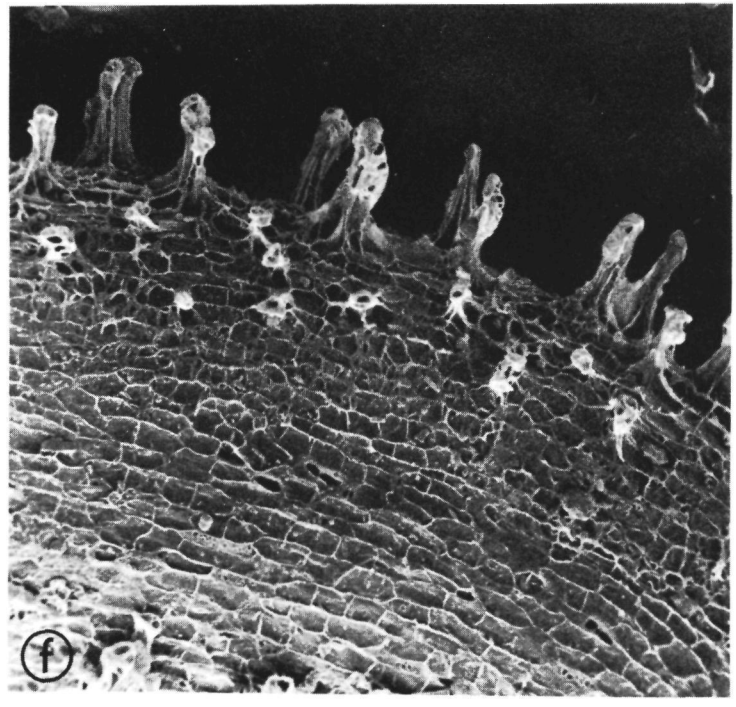
THE NETHERLANDS



CAMARGUE,
FRANCE



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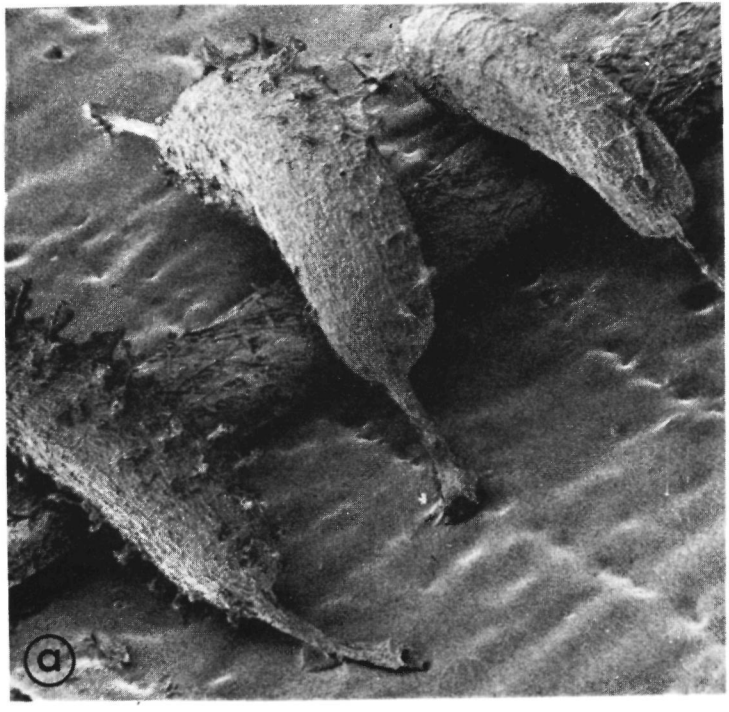

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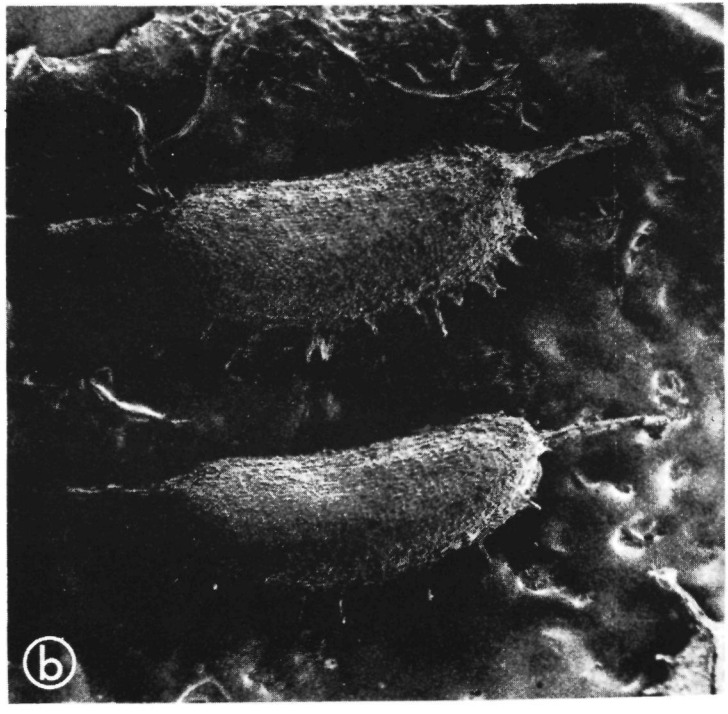
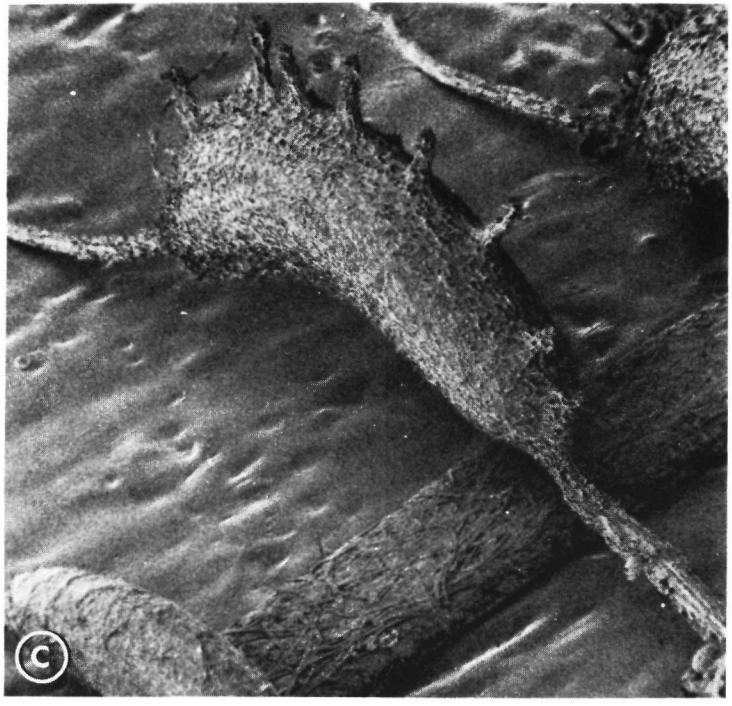
THE NETHERLANDS



NAMNSHOLMSSUNDET,
FINLAND



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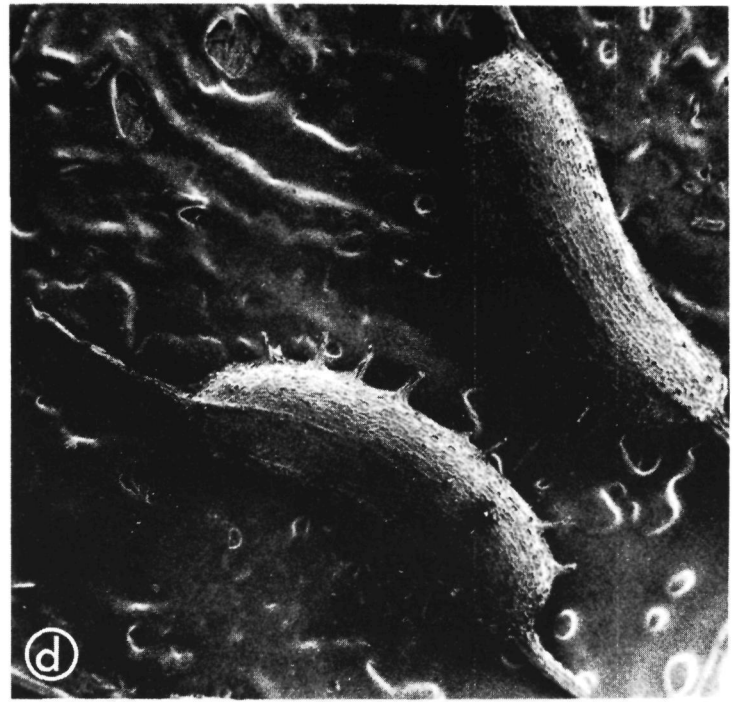

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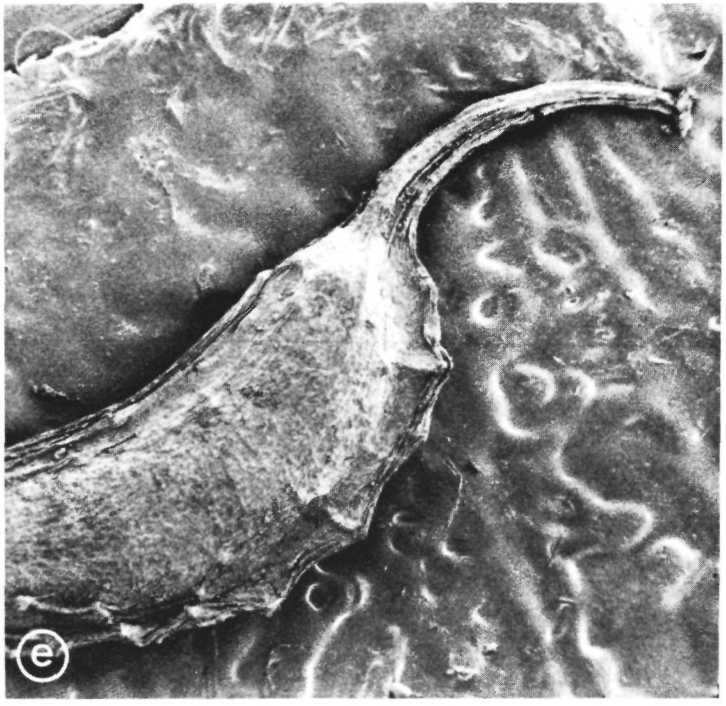
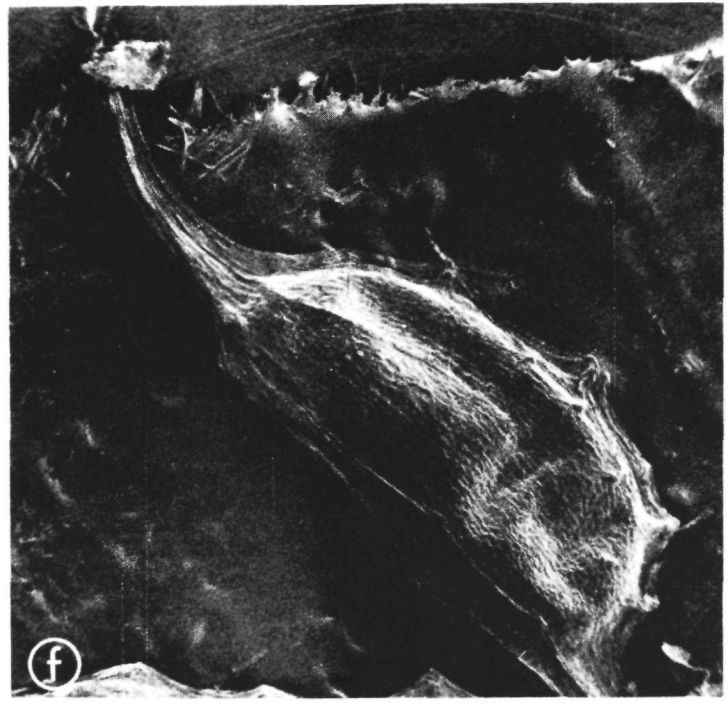


HOORN,
THE NETHERLANDS



HENRIKSBERG,
FINLAND

population seeds with and without teeth on the convex backside can be recognized; this is often due to differences in age (decaying structures). It can be clearly recognized in Fig. 4B that the seeds of *Z. major* completely differ from the seeds of the other taxa discussed. The scalloped margin at the backside of these seeds is characteristic as well as the length/width ratio of these seeds. Although the colour of the fruits of *Z. palustris* and *Z. pedunculata* is usually green it can vary to a certain extent, depending on the locality where they are developing. Small plants in shallow littoral environments are often sanded over, then fruits located near the rhizome part of these plants get buried and become white. The fruits of *Z. major* are of a typical brownish colour.

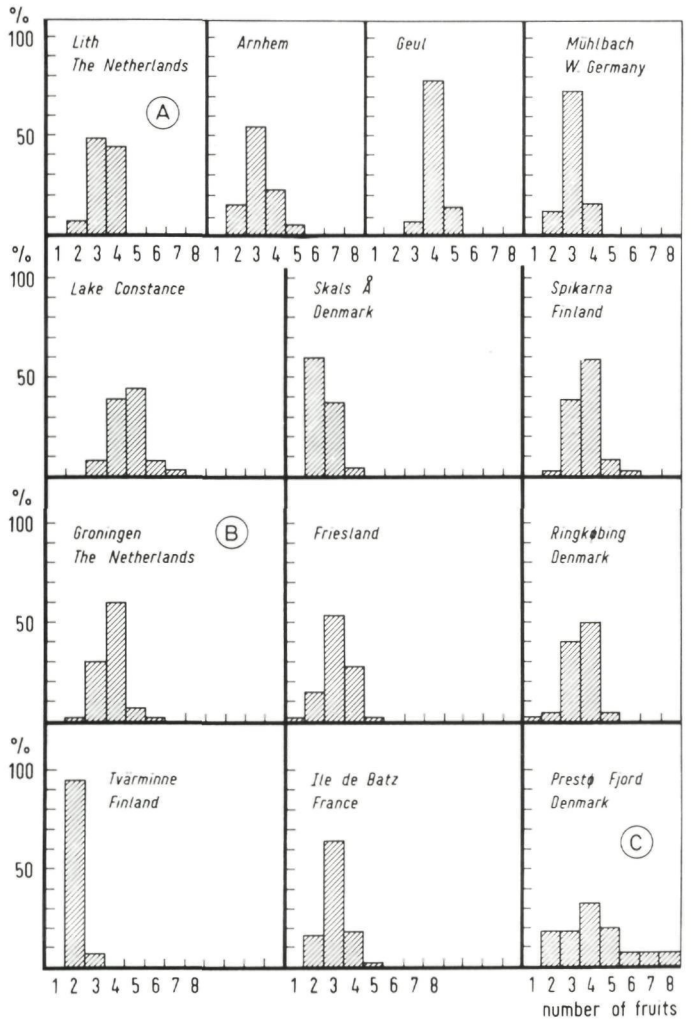


Fig. 5. Distribution of the number of fruits present in inflorescences of the different *Zannichellia* taxa in different localities in western Europe. (A, *Z. palustris* L.; B, *Z. pedunculata* Rchb.; C, *Z. major* Boenn.).

In Fig. 5, the counts of fruits in inflorescences of *Zannichellia* taxa collected in different parts of Europe are summarized. It can be concluded from this figure that the fruit number is not very suitable for identifying a certain specimen. Locally it can sometimes be used as an additional characteristic (Fig. 5; Spikarna and Tvärminne, Finland). *Z. palustris* shows a mean number of fruits per inflorescence of about three or four, with numbers regularly up to seven in Lake Constance (W. Germany). In this material even some inflorescences with 10 fruits were found. In The Netherlands *Z. pedunculata* is characterized by about three (2—6) fruits per inflorescence, while in Finland it is characterized by the lower and rather constant number of two. *Z. major* can be polycarpous.

The arrangement of the fruits is shown in Fig. 6. From this figure, a good impression of the general appearance of the fruits as found in nature is obtained. *Z palustris* fruits are generally arranged in a very regular way; the arrangement is of a symmetrical character, especially when four fruits are present. The inflection of the rostra in *Z. pedunculata* is very characteristic (see also Luther, 1947). The large and robust *Z major* fruits are almost sessile and have reflexed rostra.

Leaf morphology

Generally speaking, *Z. major* is the most robust with leaves up to 2 mm wide. The differences in appearance between the three taxa are dependent on the geographical latitude. In Tvärminne (Finland) the leaves of *Z. major* are up to 2 mm wide, in contrast to those of *Z. palustris* and *Z. pedunculata*, which are about 0.3 mm wide. The stems of *Z. major* are about 0.9 mm thick and the horizontal runners up to 1.4 mm. Both these plant parts are more slender in the case of *Z. palustris* and *Z. pedunculata* (0.4 mm). In Denmark *Z. major* can be as robust as in Finland but the author has also seen less robust material (± 1 mm wide leaves) that undoubtedly belongs to *Z. major.* In The Netherlands *Z. palustris* has a maximum leaf width of 0.5 mm, and a maximum thickness of both stem and rhizome of 0.5 mm, while *Z. pedunculata* is much more robust with leaves up to 1.5 mm wide, stems up to 0.8 mm thick and rhizomes up to 1.0 mm thick. It was very striking that *Z. palustris* material collected in the Mühlbach (W. Germany) was less fragile than the material collected from sites in Lake Constance (W. Germany). The relatively robust character (± 0.7 mm wide leaves) of the former material can be regarded as a consequence of environmental conditions, as the plants raised experimentally from seeds originating from this locality were not robust but slender, looking very similar to those collected in Lake Constance (W. Germany). The *Z. palustris* plants from running waters in The Netherlands have a striking resemblance to plants from the same type of habitat in W. Germany. In Denmark *Z palustris* was also found in running waters, but due to the lower stream velocities, these plants had longer upright shoots and were less compact than plants from the Geul (The Netherlands) and the Muhlbach (W. Germany). Several authors doubt whether the small and finely structured *Zannichellia*

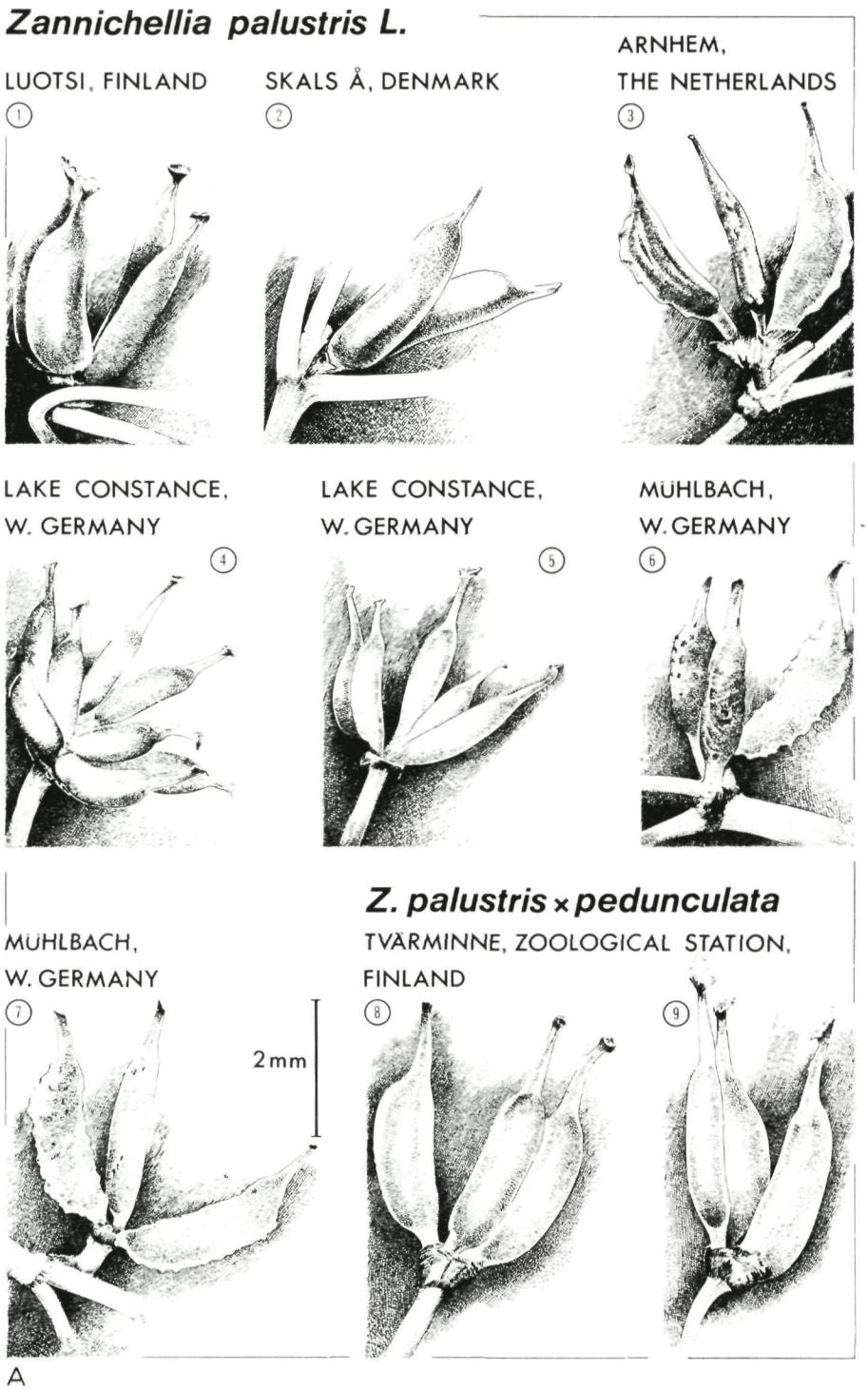
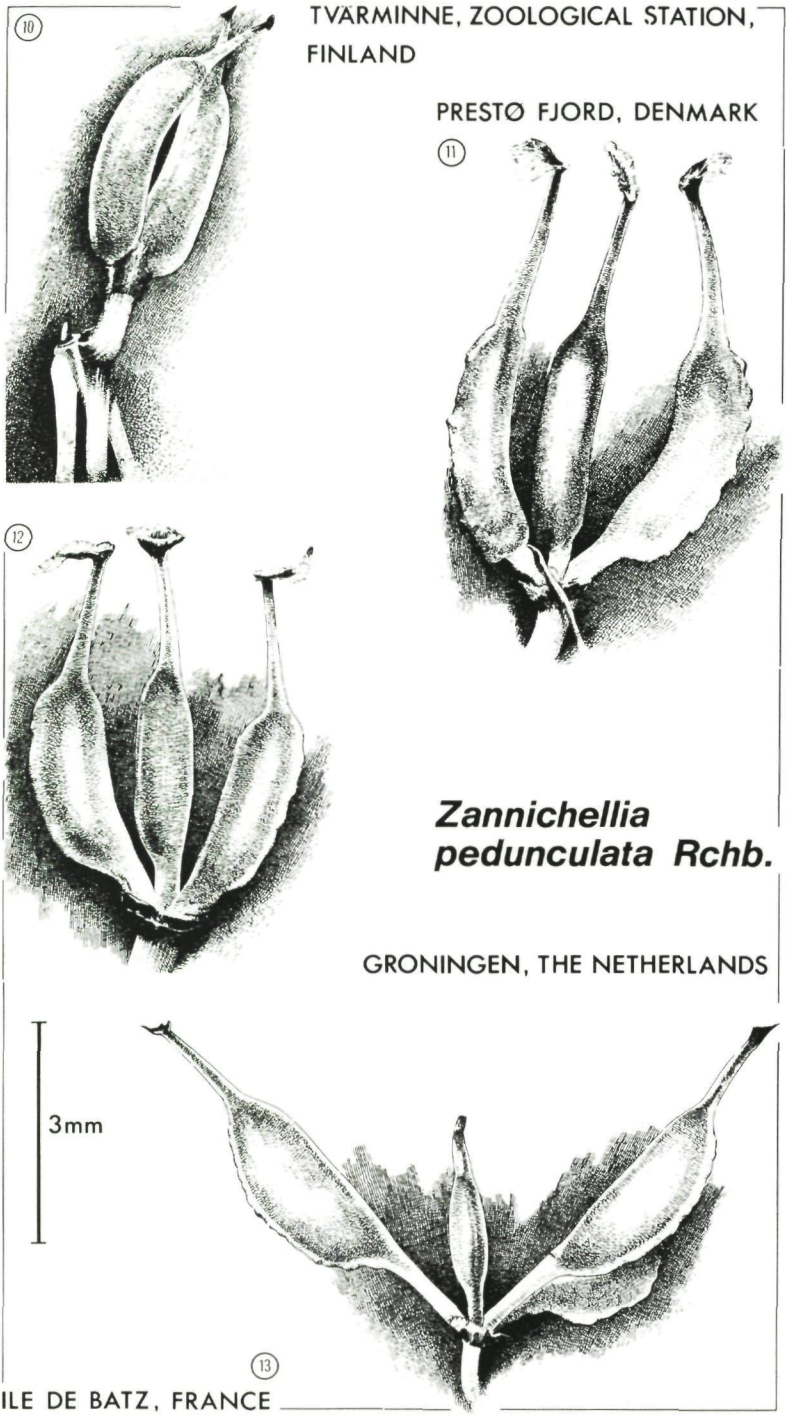


Fig. 6 (A—C). General appearance of fruits in *Zannichellia* material.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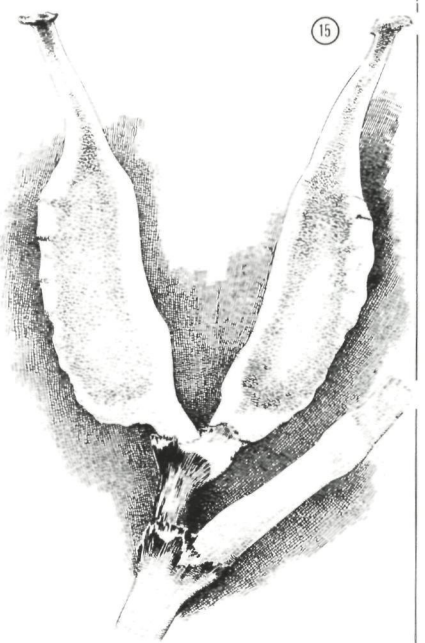
TVÄRMINNE, ZOOLOGICAL STATION, FINLAND
PRESTØ FJORD, DENMARK
11
12
Zannichellia pedunculata Rchb.
GRONINGEN, THE NETHERLANDS
3mm
13
ILE DE BATZ, FRANCE

HENRIKSBERG, FINLAND

HENRIKSBERG, FINLAND



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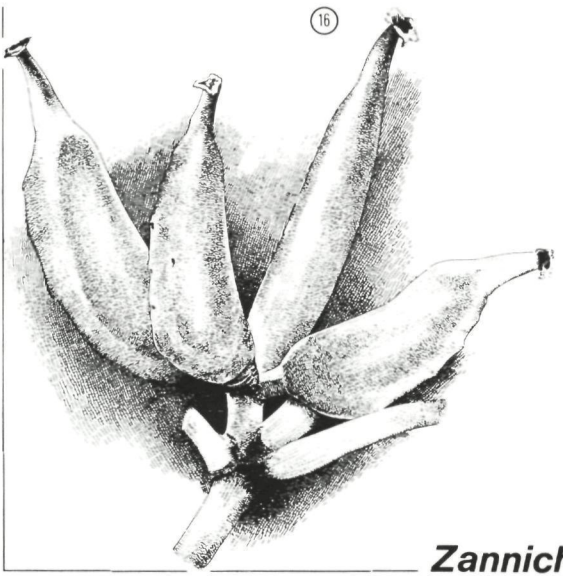


4 mm

Zannichellia major Boenn.

C

plants found exclusively in the shallow border zone of lakes such as Lake Constance (W. Germany) are identical with those found in deeper waters (Baumann, 1911; Lang, 1973).

Growth form

The growth pattern of *Zannichellia* taxa is schematized in Fig. 7. Although in the field local environmental factors can conceal this pattern to a large extent, the scheme given is representative of the general pattern of development. According to Posluszny and Tomlinson (1977), *Zannichellia* has "a creeping rhizome giving rise to complex sympodial floral shoots". In Fig. 7C the mode of formation of the horizontal propagation is illustrated. After the initial development following germination, a main rhizome axis is developed. On this axis rootless, shootless nodes alternating with nodes with roots and vertical shoots can be distinguished. The lateral development of the shoots is alternate. The vertical shoots start rooting at the first successive node and the side axis thus formed is characterized by the absence of a shootless node. Figure 7B illustrates the resultant growth pattern. In Fig. 7A, the development of a seedling of *Z. pedunculata* during a 48-day period is given. The mean shoot length increase over the mentioned period is 17 cm day^{-1}. The rhizome increased at a mean length of 2.8 cm day^{-1}. It is clear that the horizontal propagation is mainly in one direction. The dying off of some older plant parts

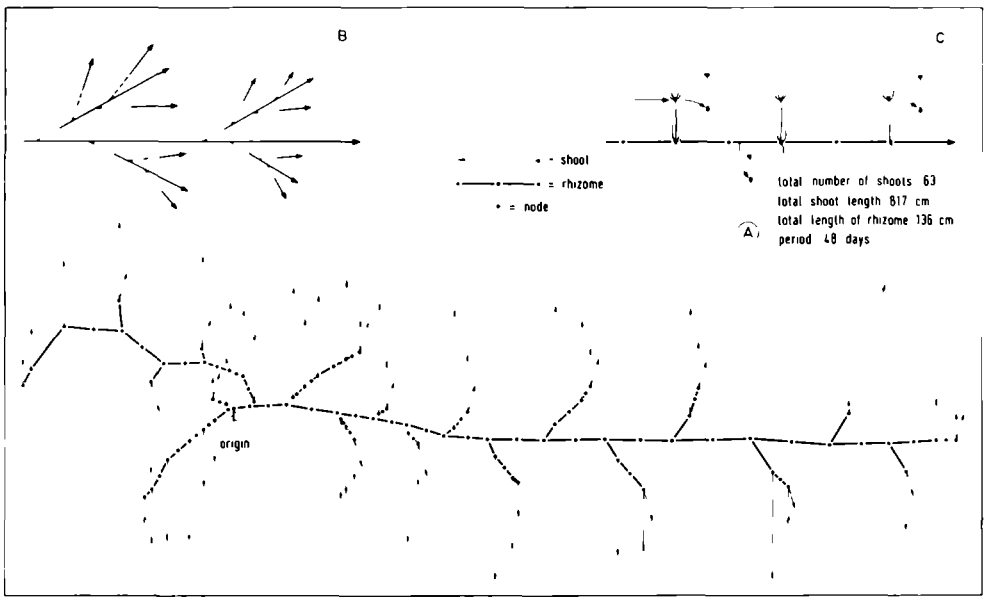


Fig. 7. (A) Growth pattern of a *Z. pedunculata* Rchb. specimen under controlled conditions (scale, shoot length:rhizome length = 3:1). (B) Branching system (- - - -, nodeless rhizome parts, ———, rhizome parts with nodes). (C) Schematic representation of the mode of formation of lateral shoots.

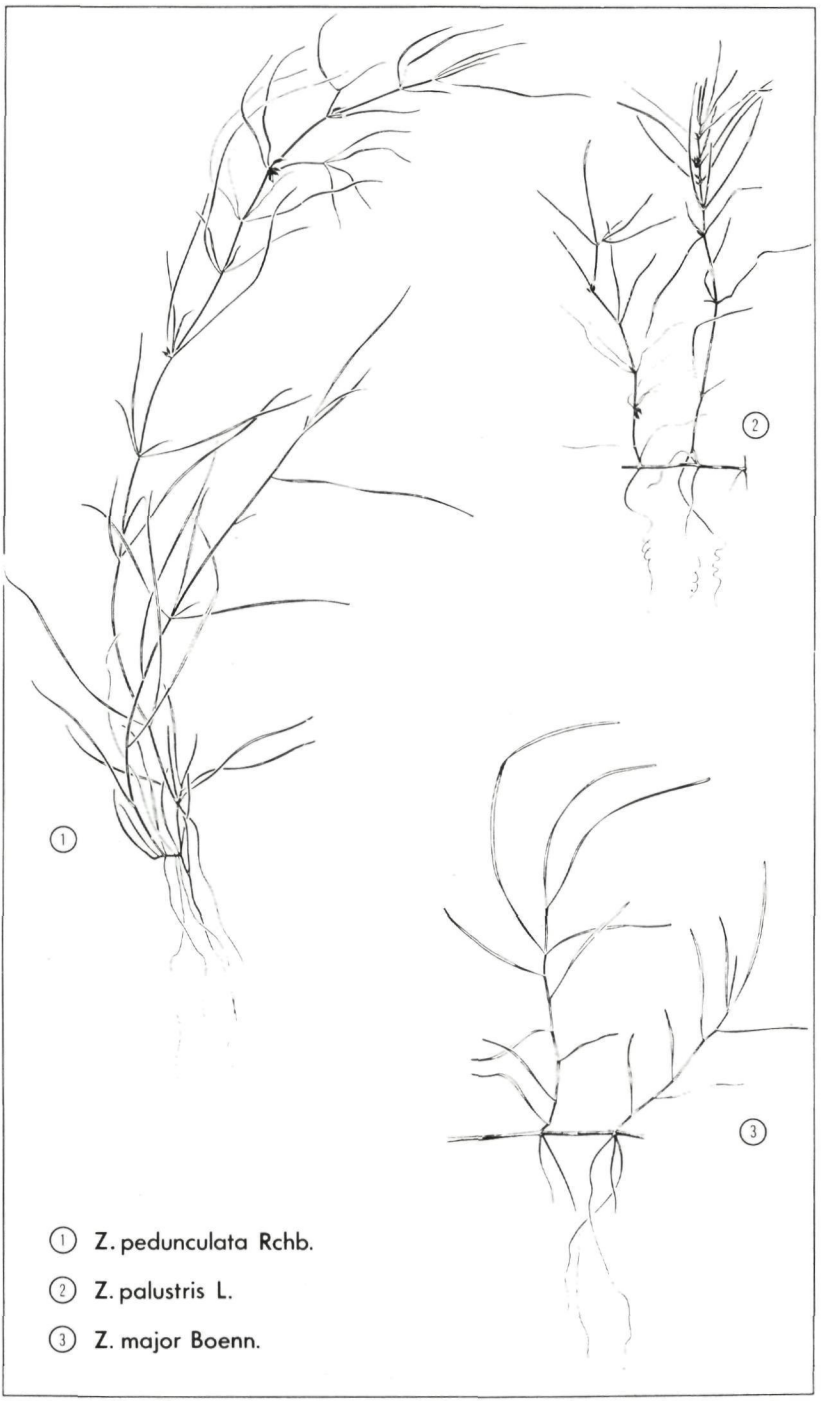


Fig. 8. General appearance of (1). *Z. pedunculata* Rchb., (2) *Z. palustris* L. and (3) *Z. major* Boenn.

caused fragmentation at the end of the recording period. In Fig. 8, the general appearance of the three taxa distinguished is given. *Z. palustris* is characterized by rather short shoots, in contrast to *Z. pedunculata*; both plants were cultured in the same aquarium under the same conditions.

Pollen grains

The pollen grains of *Zannichellia* are heavier than water and self-pollination is likely to occur. Roze (1887) described this procedure and pointed out that the diameter of the pollen grain doubles when it leaves the anther (from 15 μm to 30 μm). He also presented some drawings of these grains. Hochreutiner (1896) stated that the pollen grains are globular in shape and without any structures on the surface. Fischer (1907) also described an almost smooth exine. As shown in Fig. 9, the exine actually shows a reticulate pattern of small ridges. Pollen grains of the *Zannichellia* taxa were studied separately, but no significant differences in shape, size or general appearance could be

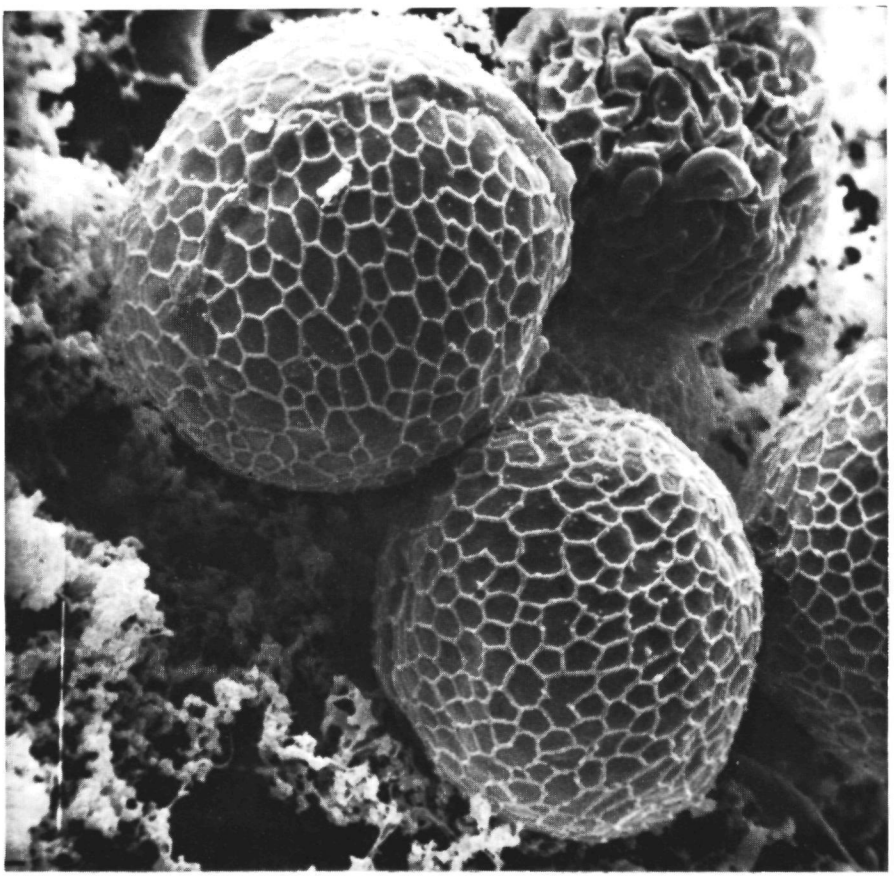


Fig. 9. Electron scanning micrograph of *Z. pedunculata* Rchb. pollen (Zeeuws-Vlaanderen, The Netherlands).

detected. A simultaneous study of the pollen of the related *Lepilaena cylindrocarpa* (Koernicke ex Walp.) Benth. showed that these pollen grains also had approximately the same diameter, shape and exine structure.

Hybrids

In the brackish waters near Tvärminne (Finland) mixed populations of *Z. palustris* and *Z. pedunculata* were studied. In such populations, specimens with intermediate characteristics were frequently encountered (see also Fig. 6A: nos. 8 and 9). Since such specimens were exclusively found in mixed *Zannichellia* populations, these intermediates are considered to be hybrids which do not seem to have the capacity of independent dispersal. The actual genesis of the hybrids was not studied. The process of pollination in *Zannichellia* would be an interesting subject for further research.

Notes on taxonomy

When studying the *Zannichellia* taxa, the question what was meant by *Z. palustris* L. was raised. It is not easy to trace which specimen(s) belonging to which taxon (taxa) was (were) used by Linnaeus when describing *Z. palustris*. According to Prof. H. Luther (1979, personal communication), the relevant text in Linnaeus' Species Plantarum mentions Bauhinius Pinax number 193. The material was collected in Montpellier (France). The specimen probably used for the description is present in Joachim Burser's Hortus Siccus (sheet X126) in the herbarium of the University of Uppsala (Sweden) and is *Z. palustris* in the sense used in this study. It is certain that Linnaeus used Burser's Hortus Siccus before 1753. A photograph of the material (fruits) probably used in the description by Linnaeus is presented in Fig. 10. The length of the fruit is 2.3 mm, and the width 0.9 mm. The rostrum length is 1.1 mm, whereas the podogyne has a length of 0.4 mm. When comparing the results of the morphological studies given on p. 109, it has to be concluded that this material is similar to the material described from the Mühlbach (W. Germany), the Gulp and the Geul (The Netherlands) and from Dorset (U.K.).

Within *Z. palustris* two taxa can be distinguished.

The first taxon, the ssp. *palustris*, is characterized by its very long and slender shoots which can reach lengths of more than a metre. The convex side of the fruit body is often irregularly shaped. This subspecies is distributed in the deeper parts of meso- and eutrophic lakes and running waters in central Europe. The material recorded in the preceding paragraph belongs to this taxon.

The second taxon, the ssp. *repens* (Boenn.) Koch is characterized by its very fine general morphology with shoots of only several centimetres. The fruits of this taxon are often characterized by a smooth convex side, in contrast to those of the ssp. *palustris*. This subspecies is found in the very shallow border zones of freshwater lakes and ponds. The material collected in Arnhem and Lith (The Netherlands), Ringkøbing Fjord, Klejtrup Sø and the Skals Å

Fig. 10. Seeds of type specimen of *Z. palustris* L. from Joachim Burser's Hortus Siccus (sheet X 126), Herbarium of the University of Uppsala, Sweden.

(Denmark), Namnsholmssundet, Spikarna and Luotsi (Finland) belongs to this taxon. *Z. palustris* ssp. *repens* occurs mainly in the northern part of western Europe.

Z. major and *Z. pedunculata* are treated according to Luther (1947, morphology and nomenclature) and Reese (1967; morphology and chromosome numbers). In Table I, the morphological and karyological characteristics for the identification of the west European *Zannichellia* material are summarized. *Z. peltata* is included in this table. The exact identity of this taxon is still under investigation but its validity is well established on the ground of the characteristics given in Table I. *Z peltata* is exclusively distributed in the southern part of western Europe

CHROMOSOME NUMBERS

Material and methods

The root tips of seedlings of the different taxa were fixed in Carnoy mixture and stained in aceto-orcein at about 50°C for 5 min (for a description of the method see den Hartog et al., 1979). The root tips were squashed and the chromosomes were counted (phase contrast microscope, 1000× magnification). However, as the chromosomes are very small and as there were hard particles in the small roots of the seedlings, it was often difficult to determine the exact number of chromosomes.

Results

Samples for chromosome counts were collected in various stations. *Z palustris* seeds from the Muhlbach (W. Germany), Lith (The Netherlands) and Namnsholmssundet (Finland) were used for the chromosome counts. The number of chromosomes was $2n = 24$. When studying *Z. palustris* material from Sherborne, Dorset (U.K.) a number of $2n = 34$ was determined. This number was obtained several times with certainty and has also been recorded by Reese (1967) in some *Z palustris* populations in northern Germany. Seeds of *Z pedunculata* were collected in the northern part (Groningen), and the south-western part (Zeeuws-Vlaanderen) of The Netherlands and from Denmark in a pool near Vester Tostrup (Jutland). These root tips all proved to contain $2n = 36$ chromosomes.

Conclusions

Reese (1967) lists all known chromosome numbers found in several parts of the world by various authors. In Bulgaria, Kozuharov and Kuzmanov (1964) found *Zannichellia* material with $2n = 12$ chromosomes. Reese (1957) mentions this chromosome number for *Zannichellia* from the Algerian Sahara.

The chromosome counts in this study agree well with the data in litera-

ture. In general, the material identified as *Z. palustris* proved to contain $2n=24$ chromosomes, whereas *Z. pedunculata* had $2n=36$ chromosomes. *Z. major* was not studied but according to Reese (1967), this taxon has $2n=32$ chromosomes. Because of the aneuploid character of *Z major*, this taxon needs some further karyological research. It has to be stated that in *Z. peltata* material collected in Spain and France (Camargue) the chromosome number $2n=12$ was found (see also Löve and Kjellqvist, 1973; van Vierssen and van Wijk, 1982). The results of the chromosome counts strengthen the evidence that three of the four chromosome numbers are often found within the genus *Zannichellia* in western Europe. The *Zannichellia* taxa in northern Europe are obviously polyploids of *Z peltata.* From the study of material identified as *Z palustris* s.l in herbaria from localities outside western Europe (e.g. the Middle East and South America) it can be stated that in many instances the identity of that material was difficult to determine and geographical variation cannot be disregarded A further karyological and morphological investigation of *Zannichellia* material on a worldwide scale is necessary to gain insight into the distribution patterns of the *Zannichellia* taxa.

AUTECOLOGICAL EXPERIMENTS WITH SEEDS OF *ZANNICHELLIA* TAXA

Introduction

A number of experiments with plants and seeds under controlled conditions have been performed to find out the relative importance of the various stages in the life-cycle of the different *Zannichellia* taxa. In this part of the study the autecological experiments with seeds and plants of *Z palustris* and *Z. pedunculata* are dealt with. The coupling with the field data will be discussed in Part II (see van Vierssen, 1982). In this section, the seed germination of *Z. palustris* and *Z pedunculata* will be studied in relation to chlorinity, temperature, light conditions, stratification and desiccation. These factors play an important role in their natural environment.

Material and methods

Germination experiments were set up with seeds from controlled cultures, i.e seedlings were planted in a substrate consisting of a mixture of sand and clay and after the plants had produced seeds, these seeds were used in the experiments. In each experiment seeds were put into petri-dishes (9 cm) and placed in a climate room under long-day conditions (16 h light, 8 h dark) and with white light (400 lx). The number of seeds per experiment was usually 25. The different chlorinity solutions were made by means of 'Wimex Meeressalz'.

The harmonic mean germination day index

The germination of seeds can be expressed as the germination percentage after a certain period, but also by an index called harmonic mean germination day (HMGD). This HMGD was also used by Rozema (1975) who studied the

germination of halophyte seeds. This index is defined as

$$HMGD = \frac{1}{(1/N)\sum \frac{N_t}{D_t}}$$

where N is the number of seeds used in the experiment, N_t is the number of seeds germinated between day t and $t-1$, and D_t is the day from the beginning of the experiment.

This index needs some further explanation. As Rozema (1975) stated, the HMGD index can be regarded as an indication of the germination rate. Some general aspects of the mathematical characteristics of this formula have been summarized in Fig. 11. In Fig. 11A the maximum germination in all examples is reached on the tenth day. The lines numbered 1, 2 and 3 represent arcs of different circles which can be mathematically described. Line 4 represents the case when the same number of seeds germinates each day. This figure will be used to explain the mathematical characteristics of the HMGD index because it is relatively simple to describe arcs of circles. In Fig. 11B a number of different interpretations of the concept of the germination rate are given. In one example, maximum germination is observed at the same moment in all instances. The steepest curve is considered to represent the highest germination rate. In the alternative example (Fig. 11B, inset) maximum germination is reached at different moments. In this case, the curve which indicates the maximum germination after the shortest period is considered to represent the highest germination rate. It appears that an exact definition of the germination rate concept is very important for obtaining a well defined HMGD index. This is illustrated by means of Fig. 11C and D. In these figures several mathematical characteristics of this index are illustrated. When the HMGD index is applied in the case of the situation given in Fig. 11A, the following considerations are relevant. When 50% germination is obtained in a low number of days it coincides with a high germination rate In Fig. 11C the relationship between the number of days taken to obtain 50% germination and the (log) HMGD is visualized. A high germination obviously coincides with a high HMGD index. This result seems to contradict the statement of Rozema (1975) that a low HMGD index indicates a high germination rate These contradictory results are elucidated in Fig. 11D. In this figure, the mode of formation of the HMGD indices for the corresponding curves in Fig 11A is illustrated. As can be seen, an initial rapid increase of the number of seeds which germinate (line 1) results in a relatively low contribution to the final HMGD index. As can also be seen, the relatively low number of germinating seeds during the last few days of the total period causes a relatively large increase of the HMGD index, finally resulting in the highest HMGD index. This information is very important within the scope of the study of the HMGD index. It means that when situations are compared as given in Fig. 11B (inset), the HMGD indices of the curves with the highest number of days taken to reach 100% germination will show the highest HMGD indices because

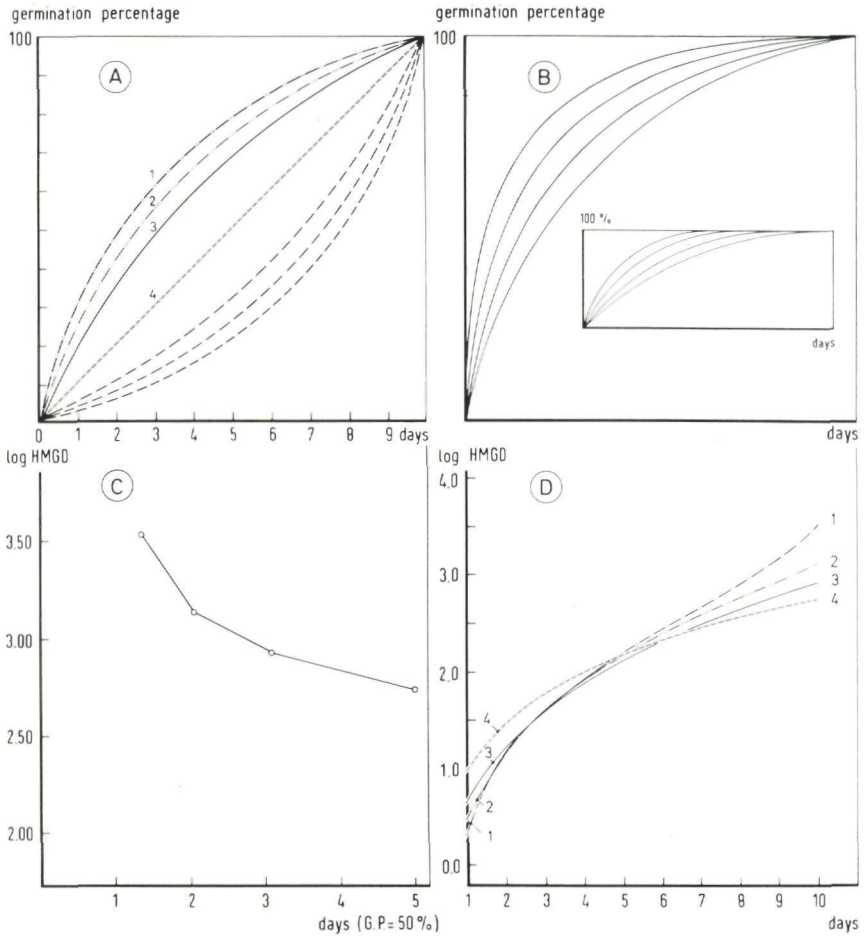


Fig. 11. Some mathematical characteristics of the harmonic mean germination day (for explanation see text).

of the enormous contribution to this index by the seeds germinating during the last part of the experimental period. As a consequence, a low HMGD index indicates a high germination rate. This index is used accordingly in this study. It has to be realized that the considerations as given above are only correct when all seeds germinate. This is, of course, not always the case. In such cases, no exact HMGD figures can be given but since a low germination rate frequently coincides with some germination after a relatively long period, the HMGD will be high in any event. It has to be stressed, therefore, that comparisons between HMGD figures can only be made when all seeds germinated. This event in most instances coincides with low HMGD figures.

The effect of chlorinity, temperature, light and desiccation on the germination of Zannichellia *seeds*

Although *Z. major* seeds germinate without delay in nature as well as under laboratory conditions (H. Luther, 1979, personal communication), no experiments were carried out with them as it was not possible to collect sufficient quantities for reliable experiments. The cultivation of *Z. major* plants for seedlings or plant parts also was not very successful. This will be discussed later in relation to field data (Part II, van Vierssen, 1982).

Germination of Z. palustris *seeds*

It was very striking that *Z. palustris* seeds collected in Lake Constance (W. Germany) during the summer months did not germinate at temperatures at which germination of *Z. pedunculata* seeds was successful. The same results were obtained with seeds from the Mühlbach (W. Germany), Lith and Arnhem (The Netherlands), the Skals Å and Ringkøbing Fjord (Denmark). To test whether the inhibited germination was caused by the physiological state of the embryo the seed coat was carefully ruptured with a scalpel. In Fig. 12 the results of the 'germination' of these seeds in relation to temperature and chlorinity are summarized. A seed was considered to have germinated when the cotyl ap-

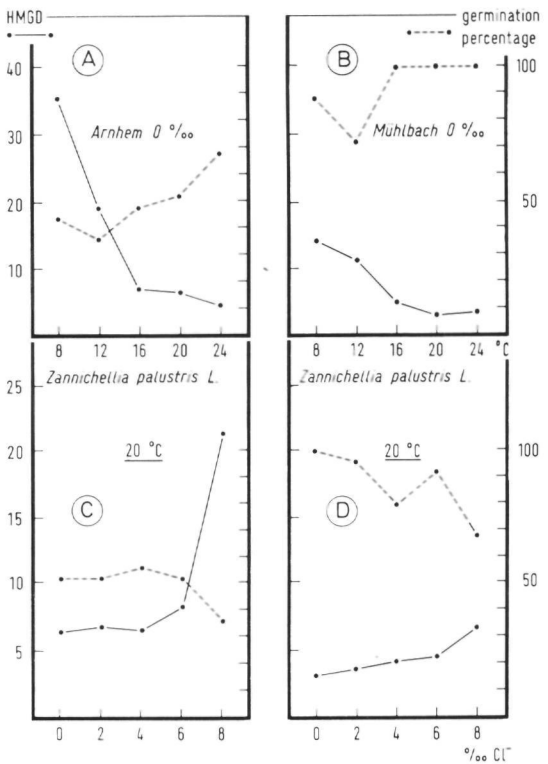


Fig. 12. HMGD and 'germination percentage' of *Z. palustris* L. seeds (ruptured) at different temperatures (°C) and chlorinities ($^{0}/_{00}$).

peared through the rupture. The embryos appeared to be viable but after some weeks the growth of the seedlings stopped and the young plants died.

Effect of redox potentials. A way to stimulate germination and to break dormancy is the application of a low redox potential, simulating the low oxygen tensions existing in the mud layer where seeds are embedded in nature. Seeds of *Z. palustris* from the Mühlbach (W. Germany) and collected in summer were deprived of oxygen (lowest redox potential of −350 mV) by means of a silt sediment mixed with organic material. After some weeks germination occurred on a small scale.

Effect of stratification. Seeds of *Z. palustris* from cultures (material from the Mühlbach, W. Germany) were stored for 2 months at 4°C. After this period germination was successful under long-day conditions (Fig. 13). The best results were obtained in freshwater at 20 and 24°C. Up to 4‰ Cl′, some germination could be recorded. At chlorinities of 6, 8 and 10‰ there was no germination at all. In the dark germination took place at a very slow rate.

Geographical variation. Because there are such large differences in the habitats in which *Z. palustris* is distributed, it is essential to test whether there is

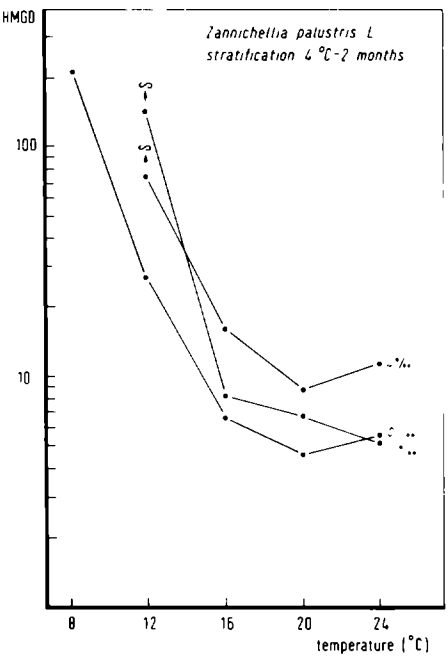


Fig. 13. Germination expressed as HMGD in relation to temperature (°C) and chlorinity (‰) of *Z. palustris* L. seeds under long-day conditions after stratification (2 months, 4°C).

any consistency in the germination ecology. In Table II, the results of a number of quick germination tests with seeds of *Z. palustris* are summarized. It appears that the observed dormancy of *Z. palustris* seeds is found in seeds from all localities listed.

TABLE II

Germination of *Zannichellia* seeds from different localities and different species before and after stratification (number of seeds 25; freshwater; long-day conditions; temperature 24°C)

Locality	Germination percentage	
	Stratification	No stratification
Z. palustris L.		
W. Germany		
Mühlbach	100	0
Denmark		
Ringkøbing	100	4
Skals A	100	4
The Netherlands		
Lith	12	0
Finland		
Namnsholmssundet	68	0
Z. major Boenn.		
Denmark		
Jungshoved	No test	56
Z. pedunculata Rchb.		
France		
Ile de Batz	No test	100
Denmark		
Vester Tostrup	No test	100
Ringkøbing	No test	52
The Netherlands		
Groningen	No test	100
Zeeuws-Vlaanderen	No test	88
Finland		
Tvärminne Zoological Station	No test	75

Germination of Z. pedunculata *seeds*

The seeds used in most experiments with *Z. pedunculata* originated from Zeeuws-Vlaanderen (The Netherlands). In Fig. 14 the results of an experiment dealing with the relation between temperature, chlorinity and the germination of *Z. pedunculata* seeds are summarized. The seeds used in this experi-

ment were not subjected to a stratification period. At all temperatures optimum germination occurred in freshwater. At low chlorinities (0 and 2‰) germination was quickest at a temperature of 24°C. At chlorinities of 4‰ and higher the optimum temperature for germination was 16°C. In Fig. 15, the germination percentages in this experiment are given. All seeds germinated at 20°C in freshwater. At 0, 2 and 4‰ germination of more than 50% often occurred. At the higher chlorinities of 6 and 8‰ germination of more than 50% was only found at the optimum germination temperature of 16°C. Non-stratified *Z. pedunculata* seeds did not germinate in the dark.

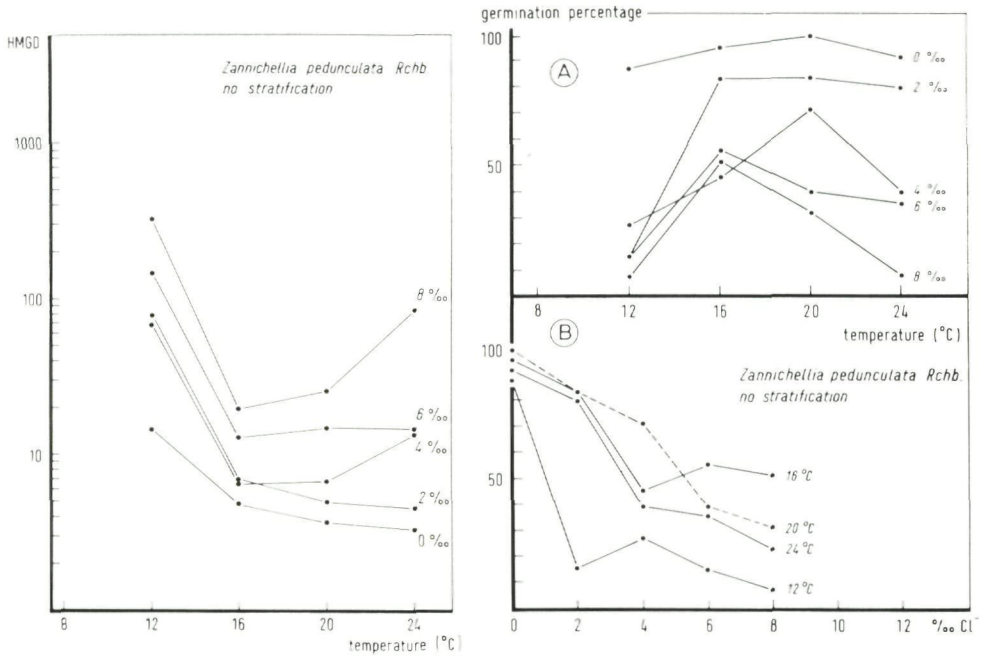


Fig. 14. Germination expressed as HMGD in relation to temperature (°C) and chlorinity (‰) of non-stratified *Z. pedunculata* Rchb. seeds under long-day conditions.

Fig. 15. Relation between germination percentage of non-stratified *Z. pedunculata* Rchb. seeds and temperature (°C) and chlorinity (‰) under long-day conditions.

After stratification (simulating winter conditions) of 2 months at 4°C, some seeds of *Z. pedunculata* were brought under the same experimental conditions as non-stratified seeds. The seeds appeared to germinate most readily in freshwater between 16 and 20°C (Figs. 16 and 17). It can be concluded (Fig. 16) that the optimum germination temperature has been lowered by this stratification process. Already at 2‰ Cl′ the optimum germination temperature was lowered to 16°C. In contrast to the situation in which no stratification took place, seed germination at chlorinities of 10 and 12‰ could be recorded with an optimum temperature of 12°C. Germination of more than 50% occurs at chlorinities of 0 and 2‰ at all tempera-

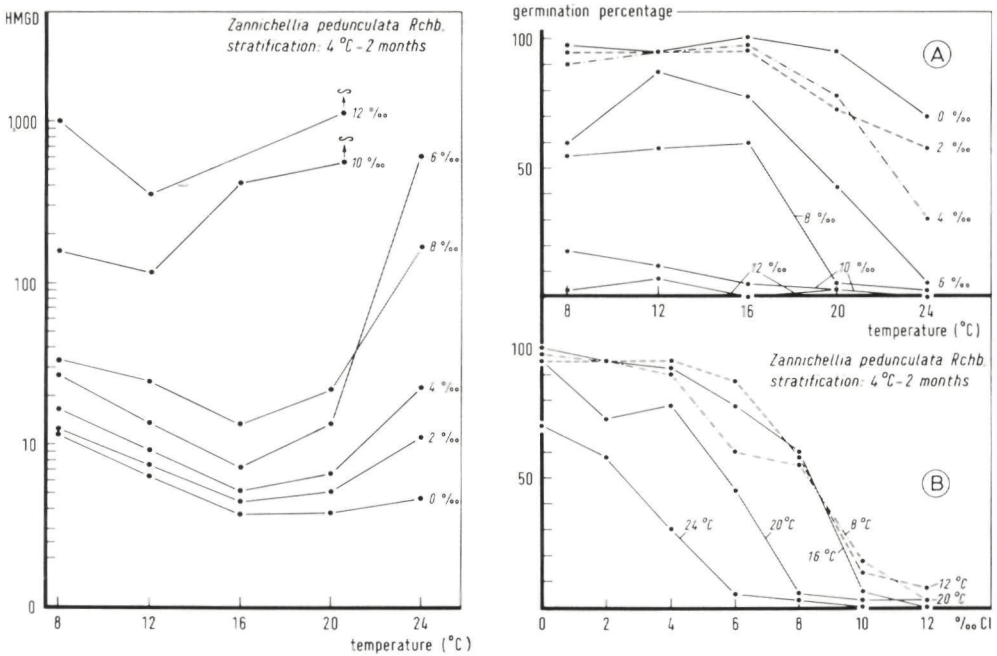


Fig. 16. Germination expressed as HMGD in relation to temperature (°C) and chlorinity (‰) of *Z. pedunculata* Rchb. seeds under long-day conditions after stratification (2 months, 4°C).

Fig. 17. Relation between germination percentage of stratified (2 months, 4°C) *Z. pedunculata* Rchb. seeds and temperature (°C) and chlorinity (‰) under long-day conditions.

tures. Even at 8‰ Cl′ the germination exceeds 50% at 8, 12 and 16°C. It is obvious that the germination is better after a stratification period. In Figs. 18 and 19 the results of germination after stratification in the dark have been summarized. Apart from a somewhat slower germination compared with the germination under long-day conditions, at 0‰ Cl′ there is a further shift of the optimum temperature towards 16°C. At chlorinities higher than 8‰ this optimum can be found at 12°C. In Fig. 20A, B and C, the shifting of the optimum germination temperature has been graphically expressed.

Effect of high temperatures. The germination of seeds was tested at temperatures up to 32°C. At this last temperature, no germination occurred. The non-stratified seeds used for the germination experiments under long-day conditions at 32°C were placed at a temperature of 16°C at the original chlorinities. The results are summarized in Fig. 20D and G and compared with the results from the germination experiment with non-stratified seeds at 16°C and long-day conditions as discussed earlier. These results can be seen in Fig. 20E and F. The exposure to the relatively high temperature of 32°C results in a somewhat better germination.

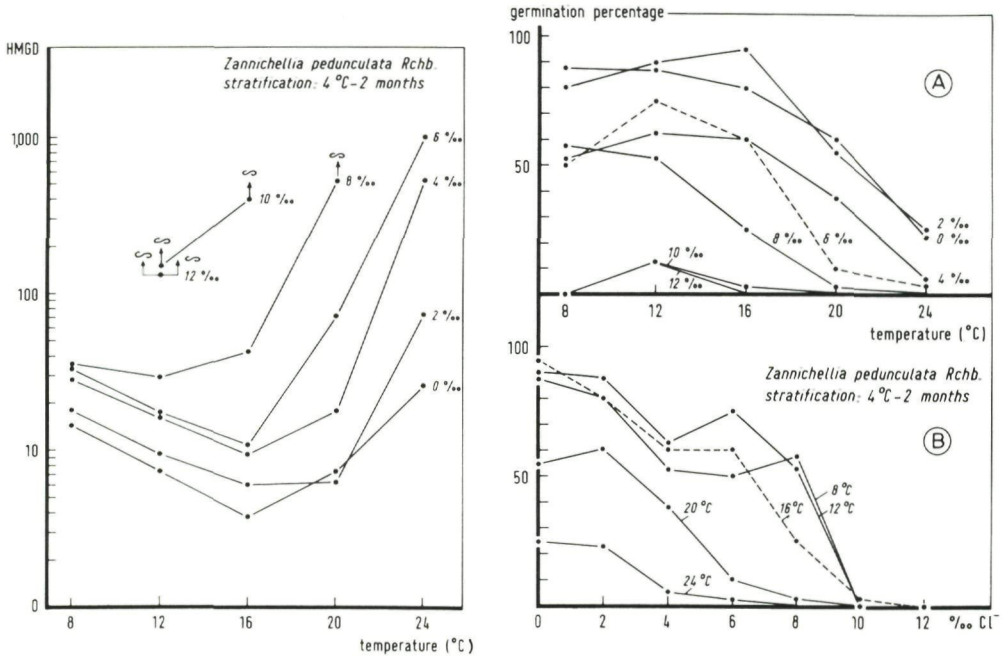


Fig. 18. Germination expressed as HMGD in relation to temperature (°C) and chlorinity (‰) of *Z. pedunculata* Rchb. seeds in the dark after stratification (2 months, 4°C).

Fig. 19. Relation between germination percentage of stratified (2 months, 4°C) *Z. pedunculata* Rchb. seeds and temperature (°C) and chlorinity (‰) in the dark.

Effect of high chlorinities. The seeds of *Z. pedunculata* which were stratified and exposed to 10 and 12‰ Cl′ under long-day conditions and in the dark but failed to germinate were placed in freshwater at the same temperatures and under the same light regimes to see if they had been damaged by these chlorinities. The results of this experiment are given in Fig. 21. When comparing these results with those obtained in the original experiment (summarized in Figs. 16 and 17), the conclusion can be drawn that no damage was caused by the high chlorinities. Under long day conditions an even slightly better germination was observed. The seeds brought from 10 and 12‰ Cl′ (long-day conditions) into freshwater, germinated equally as well as seeds put immediately into freshwater. The seeds show a tendency to germinate at relatively higher temperatures after chlorinity stress.

Effect of desiccation. In nature, as was discussed by van Vierssen and Verhoeven (1982), *Z. pedunculata* often inhabits places subject to desiccation in summer. A number of experiments simulating this process were carried out. Aquaria with a clay substrate were kept at 20°C and were filled with water of 12‰ Cl′ (long-day conditions). This chlorinity was chosen as a starting

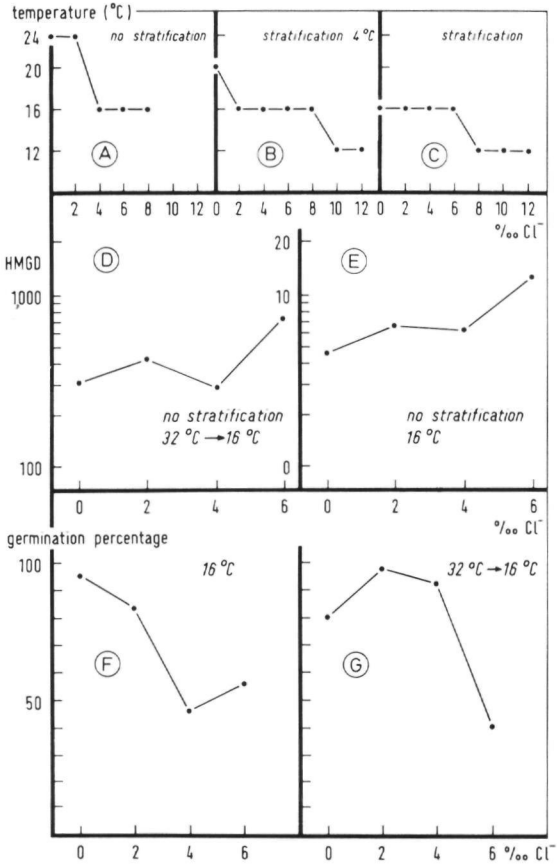


Fig. 20. Graphical representation of the decreased optimum germination temperature at various chlorinities: (A) no stratification, long-day conditions; (B) stratification, 2 months, 4°C, long-day conditions; (C) stratification, two months, 4°C, dark conditions. Comparison of the HMGD and germination percentage before (E, F) and after (D, G) a temperature shock of 32°C with a reference temperature of 16°C.

point for the experiment in which increasing chlorinity as a consequence of evaporation in summer was simulated. After some time complete desiccation occurs, but this is preceded by a short period with very high chlorinities. Seeds were exposed to four different conditions.

First, seeds were placed in water with a chlorinity of $12‰$ and a permanent character. Secondly, a number of seeds were kept under conditions of continuous evaporation which resulted in a chlorinity of at least $35‰$. A third group of seeds was kept for 1 month in a desiccated substrate with a final moisture content of less than 1.5%, and a fourth group for 3 months with a final moisture content of less than 0.5%. The seeds from the different conditions were put into freshwater at different temperatures (8, 12, 16, 20 and 24°C). The results of the following germination under long-day conditions

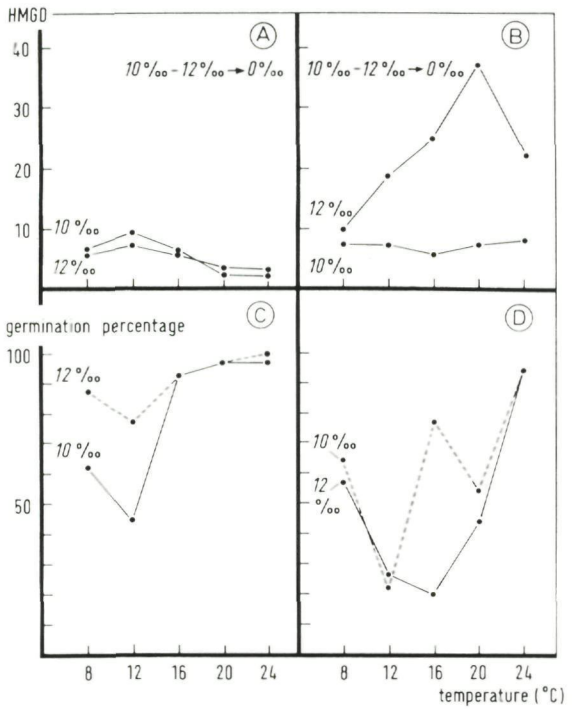


Fig. 21. Relation between HMGD and temperature, germination percentage and temperature of *Z. pedunculata* Rchb. seeds at $0‰$ Cl′ after initial failure at 10 and $12‰$ Cl′: (A, C) long-day conditions; (B, D) dark conditions.

are shown in Fig. 22A. The germination is somewhat affected by the desiccation process. There is a rapid germination in freshwater compared with the results for seeds which were not subjected to a desiccation period (see Fig. 14). The germination percentages obtained in this experiment appeared to be very high (Fig. 22C); in fact higher than 85% with the exception of one case (12°C, $35‰$ Cl′).

Another set of seeds (from the second, third and fourth group) was put under different chlorinity conditions but at a fixed temperature of 20°C. The results of the germination under the different conditions are summarized in Fig. 22B and D. Compared with the germination of seeds not subjected to desiccation (Fig. 14), it can be concluded that the chlorinity tolerance has been negatively influenced by the desiccation. The observed germination percentages are relatively low, also, after desiccation.

Effect of freezing. In order to test the tolerance of seeds with respect to freezing, 25 seeds were frozen (−5°C) under dry and wet conditions. After this treatment, no germination whatsoever could be induced.

Geographical variation. A study was made to find out whether *Z. pedunculata* seeds from other localities germinated as readily as those from Zeeuws-

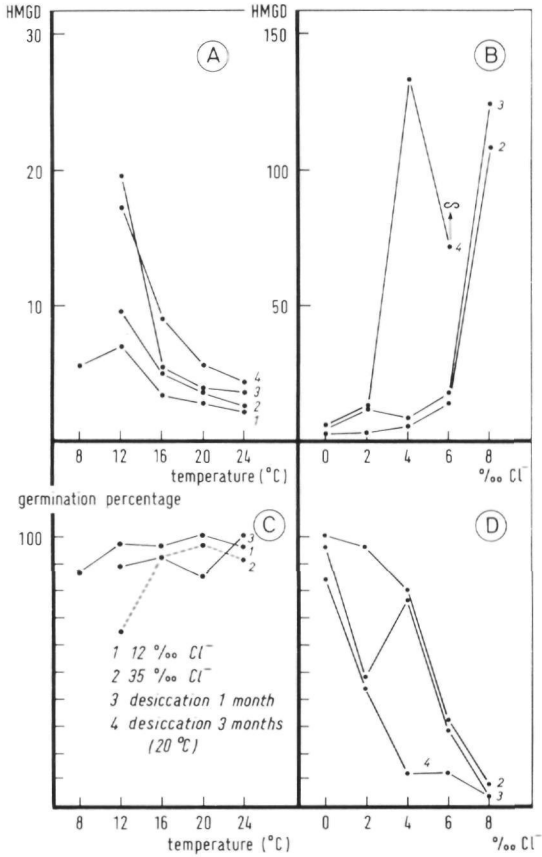


Fig. 22. HMGD and germination percentage of *Z. pedunculata* Rchb. seeds (not stratified) in relation to: (A, C) temperature at 0‰ Cl^- after different desiccation regimes (1—4). (C: 1—3, 4 omitted as it almost coincides with 3); (B, D) chlorinity (‰) at 20°C.

Vlaanderen (The Netherlands). The results agree well with the earlier results obtained with seeds of this taxon. *Z. pedunculata* seeds were collected in the Camargue (France) and plants cultured from them in The Netherlands. Seeds from this stock were used to study some general patterns of germination. There appeared to be no differences between the results obtained in the experiments with seeds from plants collected in The Netherlands and those with seeds from the Camargue. In Table II, the results are summarized from some additional easy and quick germination tests. Seeds collected from plants under field conditions were stored at room temperature under long-day conditions. After 3 weeks when no new germination of seeds could be observed, maximum germination was assessed. It is obvious that *Z. pedunculata* seeds from different localities exhibit a similar level of germination.

Discussion

Although much research has been done on the germination of land plants,

there are not many data on the germination of seeds of water plants. The most comprehensive works on this subject have been published by Guppy (1897) and Crocker (1907). Schaumann (1926) published much information concerning the seed germination of *Alisma plantago-aquatica* L., whereas Muenscher (1936) discussed this aspect for *Potamogeton* seeds. A summary of the literature dealing with this subject is given by Hutchinson (1975). Some germination experiments with seeds of the related *Althenia filiformis* Petit (Zannichelliaceae) were carried out by Onnis and Mazzanti (1971). Verhoeven (1975) found this species at a chlorinity of 8.7‰ in the Camargue (France). According to Onnis and Mazzanti (1971) germination was best at 30°C (they also tested 10 and 20°C) in distilled water. At 20°C, the germination percentages were approximately 50% at 0, 2.5 and 4.5‰ Cl' (calculated from sea water dilution factors given by the authors). At 30°C, a minimum germination percentage of 50% could be observed at chlorinities up to 9.5‰. The upper chlorinity tolerance of *Althenia* seeds is 19‰, which is much higher than the tolerances found in *Zannichellia* taxa. The optimum germination temperature of 30°C in *Althenia* is relatively high when compared with the optimum temperatures of the related *Zannichellia* taxa. It is very difficult to draw firm conclusions from these scarce literature data. It is not clear whether the mechanisms observed in the germination of *Zannichellia* seeds are widespread among aquatic macrophytes. It is obvious, however, that more information on the seed germination of aquatic macrophytes is needed. In Part II of this study (van Vierssen, 1982) the importance of germination ecology for the distribution and survival of *Zannichellia* taxa is stressed.

Conclusions

The germination characteristics of *Z. palustris* and *Z. pedunculata* differ to a large extent. The most striking difference is the dormancy of the *Z. palustris* seeds. This dormancy can be broken by a stratification period of 2 months (4°C) or a low redox potential. Then the seeds of *Z. palustris* germinate under long-day conditions at chlorinities up to 4‰. The optimum germination temperature is 24°C. In the dark only a very few seeds germinated. No differences in germination ecology between *Z. palustris* ssp. *palustris* and *Z. palustris* ssp. *repens* were recorded. *Z. pedunculata* seeds germinate without a stratification period. The best germination was observed in freshwater and at a temperature of 24°C under long-day conditions. Germination was inhibited in the dark. After a stratification period of 2 months, germination occurred at a relatively low optimum temperature of 20°C, and the chlorinity tolerance had increased up to 12‰. Germination at higher chlorinities appeared to coincide with a lowered optimum germination temperature. After a stratification period, the seeds also germinated in the dark in freshwater at a relatively low optimum temperature of 16°C. Desiccation and high temperatures (up to 32°C) do not prevent the germination of seeds. The morphological distinction of *Z. palustris* and *Z. pedunculata* is clearly coupled with essential differences in germination ecology. The results obtained in these experiments are very important

for understanding the distribution patterns in nature in relation to environmental conditions.

GROWTH AND DEVELOPMENT OF *ZANNICHELLIA* IN RELATION TO SUBSTRATE, CHLORINITY AND CHLORINITY CHANGES

As the culturing of *Z. major* was not successful, only plants of *Z. palustris* and *Z. pedunculata* were studied under experimental conditions. In the experiments the development of *Z. palustris* and *Z. pedunculata* was studied in relation to different substrates, stable chlorinities and rising chlorinities. A number of competition experiments were set up to get an impression of the behaviour of these taxa when growing in mixed stands. Such an experiment is relevant because autecological experiments with the separate species often indicate wide ecological overlaps, which usually do not occur in nature. In these experiments biomass and growth form were recorded as parameters. Much attention has been paid to the structural analysis of these species in order to develop general methods and structural parameters for the study of other representatives of the parvopotamids (*Ruppia*, *Lepilaena*, *Althenia*, certain *Potamogeton* species).

Material and methods

The plants were cultured on a substrate consisting of a mixture of sand and clay, in removable metal trays placed in glass aquaria of 60 cm × 40 cm × 40 cm (see Fig. 23). This facilitated the removal of the plants together with the substrate and abolished the handling of large and heavy aquaria. After some preliminary experiments it was found that some water movement in these comparatively small water bodies stimulated the condition of the plants. By means of small pumps (Eheim, capacity 4 l min^{-1}), the water was filtered in order to suppress phytoplankton development and to stimulate water movement. In order to prevent a mass development of epiphytes (diatoms), germanium oxide (GeO_2, 0.5 mg l^{-1}) was added to the water. Epipsammic algae were removed every week when the total water volume was renewed. The new water was first adjusted to the temperature used in the experiment (23—24°C) before being added, to avoid a temperature shock. The aquaria were subjected to a light regime of 16 h light (2500 lx) and 8 h dark.

When the development of *Z. palustris* and *Z. pedunculata* was studied in relation to the substrate, two separate experiments with these taxa were carried out in freshwater. The number of plants in each aquarium was 20.

In the experiment with plants cultured under different chlorinity regimes, *Z. palustris* and *Z. pedunculata* were planted in the same aquarium but were separated by a glass wall which enabled the medium to circulate but prevented the plants of the different taxa getting tangled. In each aquarium 10 seedlings of both taxa were planted. In the experiment in which the development of both *Zannichellia* taxa was studied in relation to a fluctuating

Fig. 23. Experimental set-up in the greenhouse, Catholic University, Nijmegen, The Netherlands.

(rising) chlorinity, the position of each plant specimen was recorded at the start of the experiment and at fixed periods plants with the same position were sampled from each aquarium and used for an interim survey. In this experiment 10 seedlings of both taxa were planted in each aquarium.

In the competition experiment four chlorinity regimes were used: 0, 2 and 4‰ and a regime starting at 0‰ with weekly increases of 1.3‰ over a 5-week period. For each regime two aquaria with mixed stands and two with monospecific stands were used. The seedlings of the two taxa were planted alternately and in four rows of four at regular distances on a mixed substrate, as used in the chlorinity tolerance experiment. Five weeks later the plants were removed and the different parameters assessed.

The structure of the plants led to some difficulties in the assessment of the parameters. A very simple and widely used parameter is the biomass of the plant material, expressed as ash-free dry weight (ADW). A disadvantage of this is that the structural aspects of the plants remain obscure. Therefore, the plants were divided into shoot and rhizome material. Further, a number of assessments were made with respect to the length of the rhizome between two successive shoots, the mean shoot length and the weight of 1 cm shoot or rhizome.

All these data were used to interpret the reaction of the plant to the given environmental conditions.

Substrate 'preference' experiment

In this experiment, substrates of a known grain size distribution were used. The type of substrate used can be determined by means of the triangle given in Fig. 24. The numbers given in this figure indicate the different substrates as used for *Z. palustris*. Substrates ranging from sand to silty clay loam were used. The duration of the experiment was 5 weeks. In this experiment *Z. palustris* plants from Lith (The Netherlands) and *Z. pedunculata* material from Zeeuws-Vlaanderen (The Netherlands) were used. In Fig. 25 the results of the experiment with respect to the assessed ash-free dry weights are given. These show that an obvious optimum biomass can be distinguished in a substrate with 15—18% clay. This type of substrate is called sandy loam. In all cases a greater biomass was produced by *Z. pedunculata*. The mean length of the rhizomes and shoots of the plants is illustrated in Fig. 26. The differences between the mean shoot lengths of these taxa are most striking. In Fig. 27, some weight data of the different plant parts are given. The rhizome parts

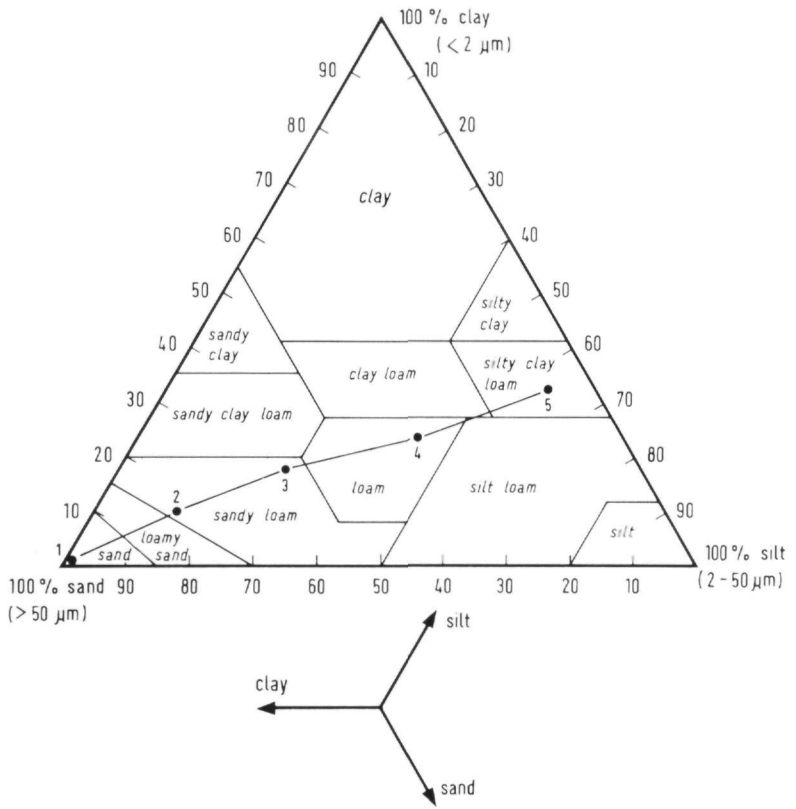


Fig. 24. Texture diagram of soils. Numbers 1 to 5 indicate the substrate gradient as used in the substrate 'preference' experiment.

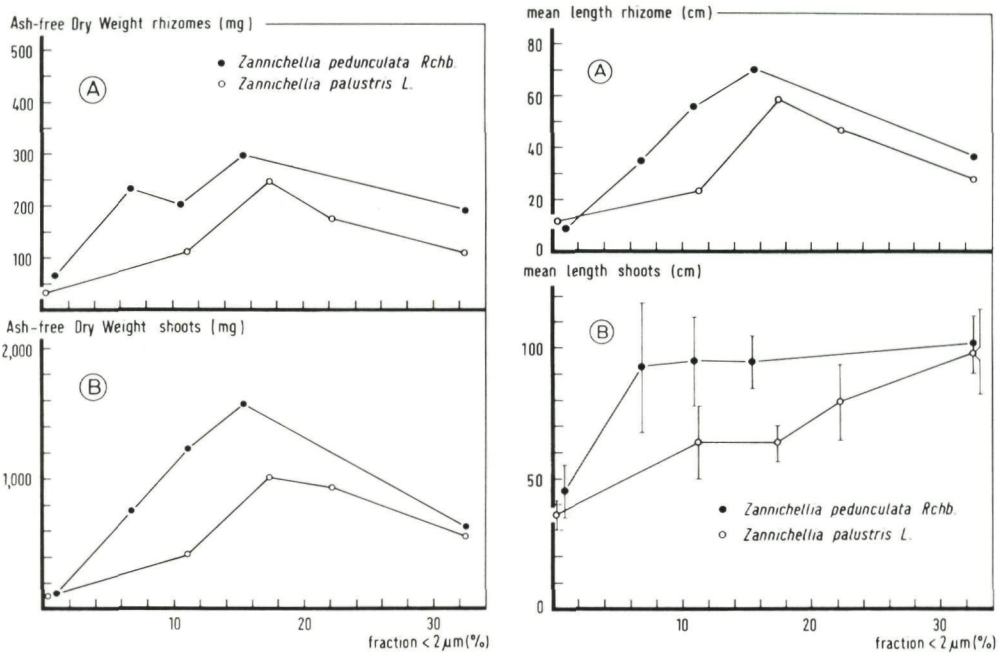


Fig. 25. Ash-free dry weight (mg) of rhizomes and shoots of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to the substrate fraction < 2 µm (%).

Fig. 26. Mean length (cm) of rhizomes and shoots of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to the substrate fraction < 2 µm (%).

vary to a large extent in weight per centimetre length, in contrast to the weight of the shoots per centimetre. These plant parts exhibit a rather constant difference in weight in favour of *Z. pedunculata.* This indicates the more robust character of the shoots of the latter. An important morphological characteristic of the *Z. palustris* plants is the production of the shoots at shorter intervals on the horizontal runners than in *Z. pedunculata* (Fig. 27C).

Chlorinity

In the experiment in which the chlorinity tolerance was tested, the optimum substrate, found in the above described experiment, was used at all chlorinities. The *Z. palustris* material originated from the Mühlbach (W. Germany), whereas *Z. pedunculata* from Zeeuws-Vlaanderen (The Netherlands) was used.

In Fig. 28 the results of the shoot and rhizome production of *Z. palustris* and *Z. pedunculata* in relation to different chlorinities are summarized. This production, especially of the shoots, was clearly highest in freshwater. In water with a chlorinity of about 10‰ the *Z. palustris* plants did not develop at all and many *Z. pedunculata* specimens died after some initial development.

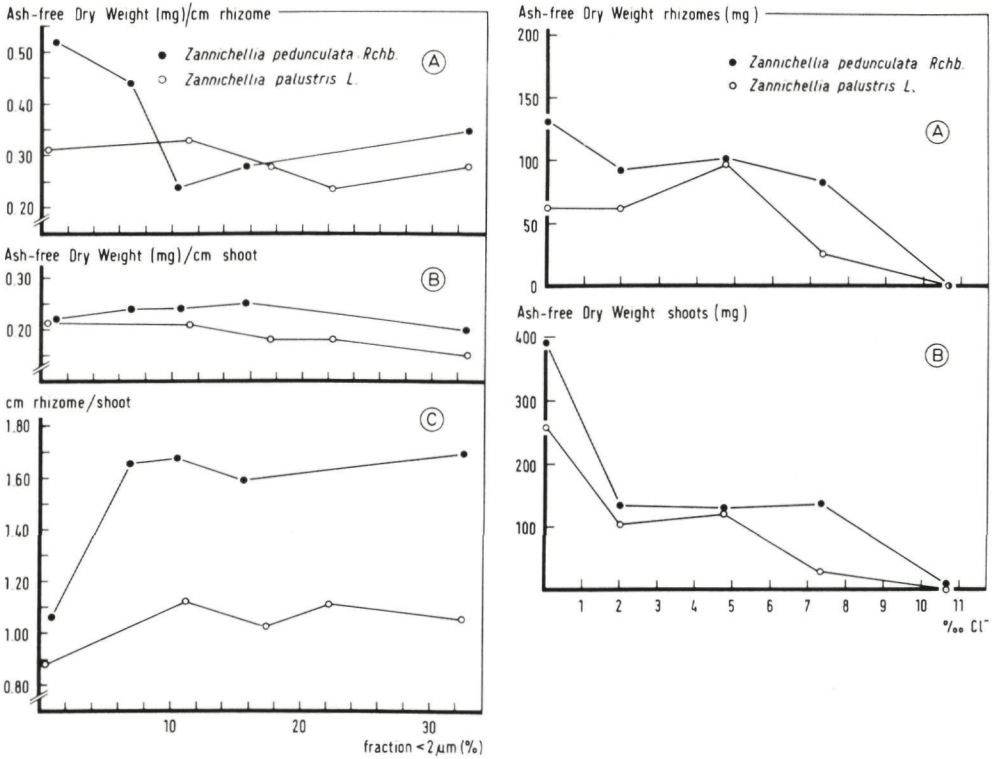


Fig. 27. Ash-free dry weight (mg)/cm rhizome, ash-free dry weight (mg)/cm shoot, cm rhizome/shoot in *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to the substrate fraction < 2 µm (%).

Fig. 28. Ash-free dry weight (mg) of rhizomes and shoots of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to chlorinity (‰).

As was found in the previous experiment, the most striking difference was the mean shoot length of the two taxa (Fig. 29A), the total number of shoots, however, did not reveal significant differences (Fig. 29B). The recorded differences in shoot biomass between the taxa were caused by the differences in shoot length.

The mean length of the rhizomes of *Z. pedunculata* exceeded those of *Z. palustris* (Fig. 30A). The intervals between the shoots are longer in *Z. pedunculata* than in *Z. palustris* (Fig. 30B).

The differences in shoot length, as discussed above, are illustrated in Fig. 31. *Z. pedunculata* tends to produce relatively longer shoots than *Z. palustris*, and this tendency becomes more evident at higher chlorinities. In Table IIIA the differences between the taxa are summarized.

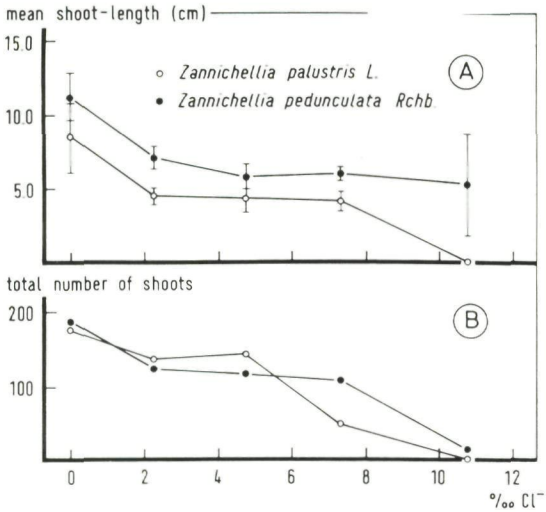


Fig. 29. Mean shoot length (cm), total number of shoots of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to chlorinity (‰).

TABLE III

Statistical parameters of different autecological experiments*

A. Chlorinity tolerance experiment with plants

‰ Cl′	Mean length rhizomes	cm rhizome per shoot	Mean shoot length	Mean shoot number per plant
0	$Pe^{++} > Pa$	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—
2.05	$Pe^{+++} > Pa$	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—
4.71	—	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—
7.24	—	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—

B. Effect of fluctuating chlorinities on plant growth and growth-form

	Pe—Pa	Shoot length	Number of shoots	Biomass
1 X 6		$Pe^{++} > Pa$	$Pa^{++} > Pe$	—
2 X 3		$P^{+} > Pa$	$Pa^{++} > Pe$	—
6 X 1		$Pe^{++} > Pa$	—	$Pe^{++} > Pa$

C. Competition experiment

	Pe^{bl}—Pa^{bl} Mean shoot length	Pe^{mi}—Pa^{mi} Mean shoot length	Pa^{bl}—Pa^{mi} Mean shoot length	Pe^{bl}—Pe^{mi} Mean shoot length
0	$Pe^{+} > Pa$	$Pe^{+} > Pa$	$Pa^{bl+} > Pa^{mi}$	$Pe^{bl+} > Pe^{mi}$
2	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—	—
4	$Pe^{+} > Pa$	$Pe^{+} > Pa$	—	$Pe^{bl++} > Pe^{mi}$

*Pe, *Z. pedunculata* Rchb.; Pa, *Z. palustris* L.; bl, blanco, monospecific stands; mi, mixed stands; +, $P < 0.10$; ++, $P < 0.05$; +++, $P < 0.001$.
(— = no significant difference)

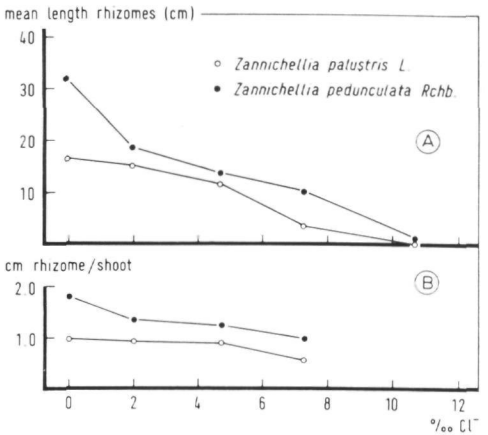


Fig. 30. Mean length of rhizomes (cm), and cm rhizome/shoot of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in relation to chlorinity (‰).

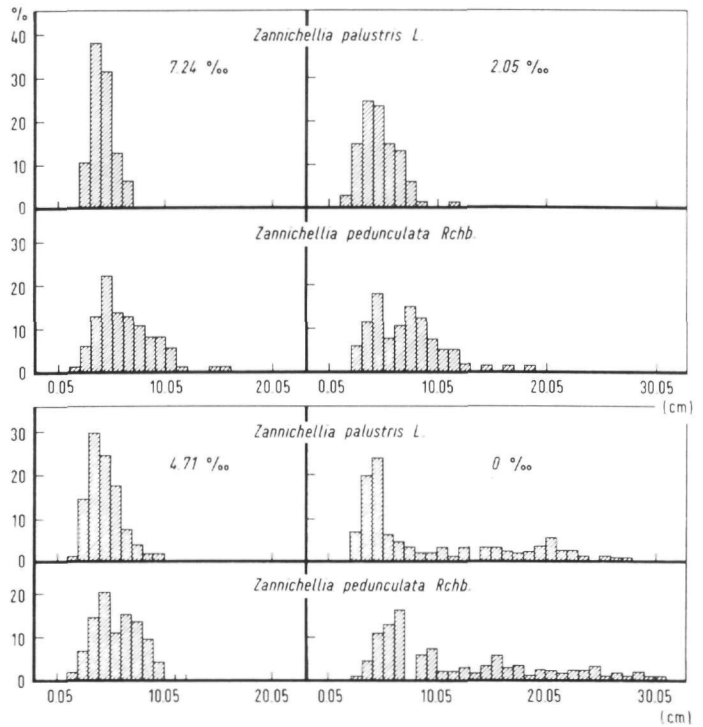


Fig. 31. Distribution of shoot lengths of *Z. palustris* L. and *Z. pedunculata* Rchb. in relation to chlorinity (‰).

The generative stage of the plants was also recorded after 5 weeks in order to collect some information with respect to the chlorinity tolerance in relation to the reproductive capacity. This information is summarized in Fig. 32. The distribution of the generative stage of the plants used in the experiment is more uniform in the case of *Z. pedunculata.* In freshwater *Z. palustris* obviously can achieve its generative cycle in a shorter time than *Z. pedunculata* under these conditions.

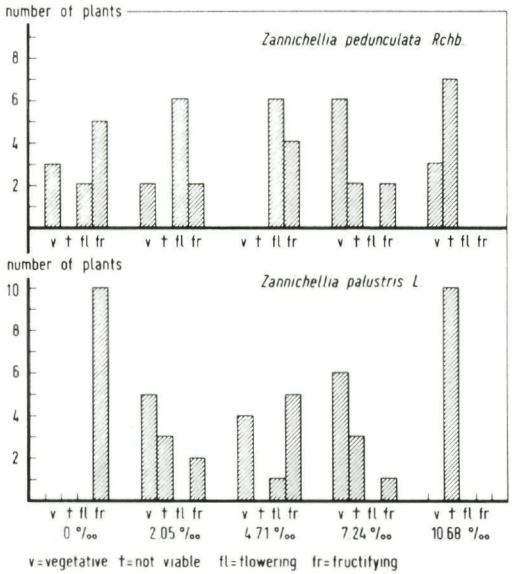
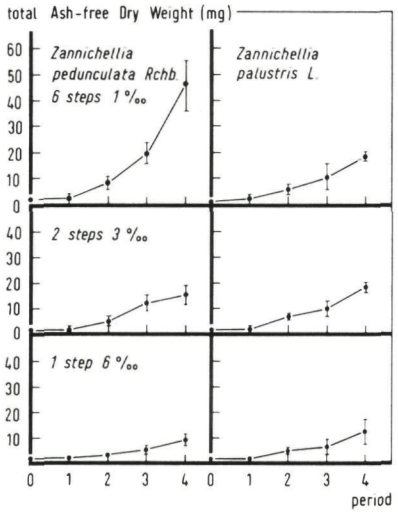


Fig. 32. Generative stage of *Z. palustris* L. and *Z. pedunculata* Rchb. in relation to chlorinity (‰) after 5 weeks.

Fluctuating (rising) chlorinity

As brackish waters are often characterized by fluctuating chlorinities, the reaction of the two taxa was tested with respect to fluctuating (rising) chlorinities. The plants used in this experiment were grown from seeds collected from the same stations as those from the chlorinity tolerance experiment. It has to be realized that in the aquarium in which the chlorinity finally reaches 6‰ after several steps of 1‰, these shocks are less severe than in the aquarium in which this chlorinity is reached by means of two severe shocks of 3‰. In both cases the average chlorinity over the whole period is about 3‰. The development of the plants expressed as increases in the ash-free dry weights are given in Fig. 33. When comparing the results for *Z. palustris* with those for *Z. pedunculata*, it can be seen that the production of *Z. palustris* was hardly affected by the increasing chlorinity, whereas the *Z. pedunculata* production differs by a factor 5 in the 6-step and 1-step regime. When studying the growth pat-

tern and general appearance of the plants in this experiment, it is again obvious that *Z. pedunculata* produces relatively large shoots (Fig. 34). Even when *Z. palustris* produces as much material as *Z. pedunculata* the mean shoot length of the second taxon remains longer. In Table IIIB, the differences between the taxa are summarized. Combining the results of this section and those of the previous one, it can be concluded that *Z. pedunculata* is obviously more chlorinity tolerant than *Z. palustris* but 'prefers' gradual chlorinity changes; *Z. palustris* shows a rather indifferent reaction towards chlorinity changes.



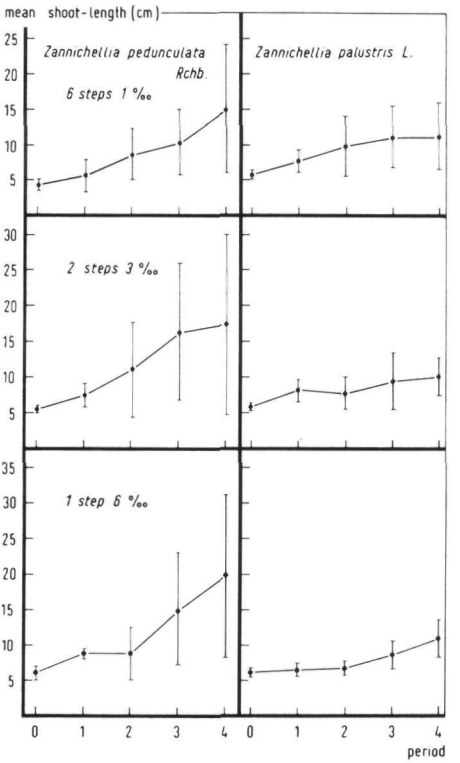


Fig. 33. Increase of ash-free dry weight (mg) of *Z. palustris* L. and *Z. pedunculata* Rchb. under different chlorinity conditions over a 5-week period.

Fig. 34. Increase of mean shoot length (cm) of *Z. palustris* L. and *Z. pedunculata* Rchb. under different chlorinity conditions over a 5-week period.

Competition

This section deals with the reactions to chlorinity stress when *Z. palustris* and *Z. pedunculata* occur in mixed stands. For this experiment *Z. palustris* was collected in Ringkøbing Fjord (Denmark) and *Z. pedunculata* material in Zeeuws-Vlaanderen (The Netherlands). As is illustrated in Fig. 35A, it is only

at 2‰ Cl′ that *Z. pedunculata* produces more material in mixed stands than in the monospecific stands under the same experimental conditions. When comparing the biomass ratios of *Z. palustris* and *Z. pedunculata* in the mixed and the monospecific stands, it is obvious from Fig. 35B that for some reason *Z. pedunculata* gains quantitative importance compared to *Z. palustris*. The difference in the ratio under fluctuating (rising) chlorinities is even more striking, this is indicated by the open and closed circles above the arrow which indicates the mean chlorinity over the experimental period. The result of competition with respect to shoot and rhizome production is given in Fig. 35C and D. In the case of *Z. palustris* competition seems to have a clear impact on the shoot/rhizome ratio (S/R). It is obvious that *Z. palustris* produces relatively less shoot material than *Z. pedunculata*. The mean shoot length is given in Fig. 36A and B. The shoot length of *Z. pedunculata* clearly decreases in mixed stands, but still exceeds that of *Z. palustris*. Under competition there is a slight increase and a clear decrease in the number of shoots per plant of *Z. pedunculata* and *Z. palustris*, respectively (Fig. 36C and D). The effect of gradually increasing chlorinity upon the shoot length of *Z. palustris* in monospecific stands is similar. The absolute dominance of *Z. pedunculata* over *Z. palustris* under such a chlorinity regime is due to the fact that the number of shoots produced by the latter is greatly reduced. This can also be observed under more stable chlorinity conditions when the taxa grow in mixed stands but the effects are not as evident as when the chlorinity gradually in-

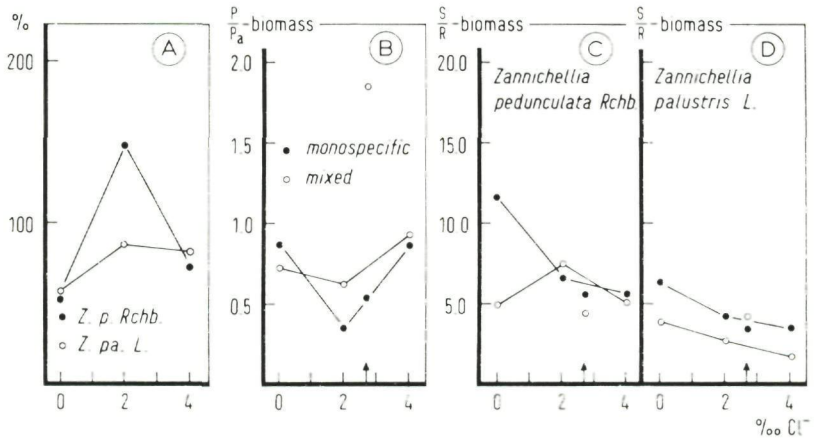


Fig. 35. Comparison of different production parameters of *Z. palustris* L. and *Z. pedunculata* Rchb. resulting from monospecific and mixed stands. (A) Comparison of the biomass production within each taxon between the monospecific and mixed stand expressed as percentage of the biomass in the monospecific stand. (B) Comparison of the biomass production of *Z. palustris* L. (P_a) and *Z. pedunculata* Rchb. (P) in monospecific and mixed stands under different chlorinity conditions. The arrow indicates the mean chlorinity in the experiment with the fluctuating (rising) chlorinity. (C, D) Comparison of the shoot (S) and rhizome biomass (R) production for *Z. palustris* L. and *Z. pedunculata* Rchb. under different chlorinity conditions in monospecific (•) and mixed (○) stands.

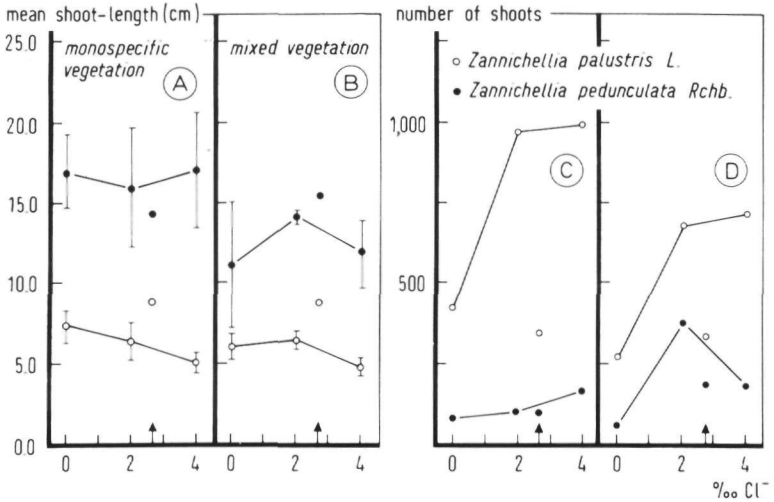


Fig. 36. (A, B) Mean shoot length (cm) of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in a monospecific and mixed vegetation under different chlorinity conditions. (C, D) Number of shoots of *Z. palustris* L. (○) and *Z. pedunculata* Rchb. (•) in a monospecific (C) and a mixed vegetation (D) under different chlorinity conditions.

creases. In general, *Z. pedunculata* is more successful in the competition for space under fluctuating (rising) saline conditions than *Z. palustris*. In table IIIC, the differences between the two taxa are summarized.

Discussion and conclusions

When discussing the results of the experiments it is important to refer to other studies. An important question is whether the differences between experiments under controlled conditions and field observations and slight differences between taxa grown under controlled conditions are relevant. There is not very much information available on experiments with aquatic macrophytes under experimental conditions. Verhoeven (1979) studied the development of *Ruppia* taxa in relation to different substrates and chlorinities, and actually found higher chlorinity tolerances for *Ruppia maritima* s.s. in his experiments than under field conditions. Bourn (1932) studied the growth of cuttings in relation to salinity. He found maximum increases in dry weights at rather high chlorinities for *Potamogeton pectinatus* L., this was at 20% sea water (± 3.8‰ Cl′) and for *P. perfoliatus* L. at 12% sea water (± 2.3‰ Cl′). *Najas flexilis* (Willd.) Rostk & Schm. was stimulated in growth between 2% (± 0.40‰ Cl′) and 4% (± 0.80‰ Cl′) sea water. The maximum salinity at which some increase of weight was still observed in the case of *P. pectinatus* and *P. perfoliatus* was 36% sea water (± 6.8‰ Cl′). *Ceratophyllum demersum* L. could stand salinities up to 24% sea water (± 4.6‰ Cl′) before the growth ceased. Haller (1974) indicated 13.3‰ S (± 7‰ Cl′) as being toxic to *Myriophyllum spicatum* L.

From these figures it follows that the absolute chlorinity tolerance limits under experimental conditions differ to a large extent and are often much higher than the tolerance limits found in the field (for chlorinity tolerance limits see Luther, 1951a). The chlorinity tolerance of *Z. palustris* from the Mühlbach (W. Germany) can be considered as relatively high. Although there is evidence from the experiments described in this study that the absolute chlorinity tolerance of *Z. palustris* is less than that of *Z. pedunculata*, it can be concluded that both taxa are very salt tolerant. However, it has to be realized that not only the tolerance limits of the vegetative plant parts are important but that the limits tolerated by the seeds, tubers or turions are also of interest. Teeter (1965) studied the influence of NaCl on the various parts of *P. pectinatus* and found different effects in plants of different ages, on seed germination, seed production, tuber growth and tuber production. This is in agreement with the author's results for *Zannichellia.*

The different effects of different salts on aquatic macrophytes is interesting. Nobel and Kohler (1978) studied the effects of Na, K, Ca or Mg salts on the net photosynthesis of species such as *M. alterniflorum* DC., *Ranunculus peltatus* Schrank and *Elodea canadensis* Michx. and found that they were very different. Although in western Europe *Zannichellia* taxa are mainly distributed in salt waters in which Na is the main cation, the observations of these authors could be of importance when studying *Zannichellia* taxa from other areas.

The results of the experiments with fluctuating chlorinities and the competition experiments indicate how important growth form is in the competition between *Z. palustris* and *Z. pedunculata.* In general *Z. palustris* has relatively shorter but more shoots than *Z. pedunculata.* The shoots are produced at shorter intervals on the rhizomes in *Z. palustris* than in *Z. pedunculata.* Under fluctuating chlorinities *Z. pedunculata* develops relatively better than *Z. palustris.*

It is a combination of these characteristics and the decrease in the number of shoots produced by *Z. palustris* under fluctuating chlorinities that is fatal for it in the competition for space with *Z. pedunculata.*

EVALUATION OF THE RESULTS

This study clearly justifies the subdivision of *Z. palustris* L. s.l. The morphological characteristics of the taxa distinguished are subject to certain geographical variation, but studied on a local scale the differences are always obvious. A main characteristic in the distinction of the species is the fruit morphology. The length ratio of the rostrum and fruit is relevant in the distinction of *Z. palustris* and *Z. pedunculata. Z. major* differs from these taxa in many ways.

Three of the four chromosome numbers established confirm the available information that at least three numbers are present in the west European populations; $2n=12$ (*Z. peltata*), $2n=24$ (*Z. palustris*) and $2n=36$ (*Z. pedunculata*). The number recorded for *Z. major* ($2n=32$) still needs some further research.

The results of the germination experiments confirm that at least *Z. palustris* and *Z. pedunculata* are separate taxa. *Z. major* was distinguished on rather negative grounds, as it appeared to be impossible to cultivate. *Z. palustris* seeds were uniform in their dormancy. This dormancy could be broken by a stratification period of 2 months at 4°C. After this procedure, germination occurred under long-day conditions. *Z. pedunculata* germinated best in freshwater under long-day conditions. At $10^0/_{00}$ Cl′ germination ceased. A stratification period of 2 months (4°C) permitted germination in the dark and resulted in a lower optimum germination temperature. High temperatures, up to 32°C, and high chlorinities inhibited germination but did not damage the seeds. Cultivation experiments with *Z. palustris* and *Z. pedunculata* indicated that the growth of these taxa was best on sediments with a high clay content. The chlorinity tolerance of the plants of both taxa did not differ very much. No great damage was observed up to $6^0/_{00}$ Cl′. The absolute tolerance limit of *Z. palustris* was somewhat lower than that of *Z. pedunculata.*

When mixed stands of *Z. palustris* and *Z. pedunculata* are exposed to chlorinity fluctuations, *Z. pedunculata* dominates *Z. palustris* because of the better salt tolerance and its characteristic growth-form.

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THE ECOLOGY OF COMMUNITIES DOMINATED BY *ZANNICHELLIA* TAXA IN WESTERN EUROPE. II. DISTRIBUTION, SYNECOLOGY AND PRODUCTIVITY ASPECTS IN RELATION TO ENVIRONMENTAL FACTORS

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ABSTRACT

Van Vierssen, W , 1982 The ecology of communities dominated by *Zannichellia* taxa in western Europe II Distribution, synecology and productivity aspects in relation to environmental factors *Aquat Bot*

The distribution of three *Zannichellia* taxa is discussed in relation to environmental factors such as chlorinity, size of the habitat, desiccation, water depth, water circulation and climatic conditions

Zannichellia palustris L occurs in northern, central and western Europe, the coastal zone of the last area excepted In the Baltic area it occurs in brackish as well as freshwater habitats The chlorinities recorded indicate a tolerance limit under field conditions of up to ± 3 5‰ To the south, in The Netherlands, it is confined to freshwater The germination ecology indicates an obligate stratification period (at 4°C) of two months to achieve germination and this climatic condition is found in the area in which this taxon occurs The growth form (short but numerous vertical shoots) allows a development in very shallow and ephemeral freshwater habitats

Zannichellia pedunculata Rchb reaches its optimum development in the coastal area of western Europe Many of its habitats are subject to desiccation during the summer months and generally show chlorinities of less than 6—7‰ In southern Europe chlorinities of 10‰ are tolerated Its seeds germinate very well in summer without stratification The seeds do not germinate in the dark, this inhibition disappears after a cold period and the optimum germination temperature then appears to be lowered The drought resistance is very high Its distribution in temporarily dry habitats (± 50% of the *Zannichellia* habitats in the Camargue, ± 22% in The Netherlands) can be understood by these phenomena

Zannichellia major Boenn is a perennial, and occurs only in northern Europe where it is confined to dynamic waters with strong water circulation and a rather stable chlorinity between 2 5—11‰

A number of community types were distinguished on the basis of their floristic composition In western Europe four *Z palustris* communities were recognized in stagnant freshwaters and two in running waters

In the Baltic area (Finland, Denmark) five brackish water communities with *Zannichellia* taxa were distinguished, in The Netherlands four brackish-water community types with

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Z. pedunculata and in the Camargue two brackish-water types with this taxon. Important and frequently encountered accompanying aquatic macrophytes are *Potamogeton pectinatus* L., *Potamogeton pusillus* L., *Ranunculus baudotii* Godr., Characeae and, in mesohaline waters, *Ruppia maritima* L var. *maritima*

The macroscopic fauna inhabiting the phytocoenoses was studied qualitatively and quantitatively (numbers and biomass). The number of species in this fauna ranged from 30 (maximum of a community type) in isolated pools, up to 70 in semi-isolated permanent brackish waters in The Netherlands. Except for the situation in the Baltic area, the species composition is dominated by freshwater insects. The diversity index H' (Shannon—Weaver) ranged from 0.61—2.37 for the numbers of animals, and from 0.86—2.71 for the biomass. The number of animals inhabiting the phytocoenoses ranged from 700—28,800/m² and their biomass from 150 up to 22,900 mg ash-free dry weight/m².

The macrophyte biomass was also assessed. The maximum seasonal biomass recorded for a phytocoenosis (mixed vegetation stand) was between ± 70—± 300 g ash-free dry weight/m². The highest biomass of a monospecific *Zannichellia* stand (*Z. pedunculata*) ever found was 246 g ash-free dry weight/m².

Generally, the *Zannichellia*-dominated communities have a more diverse fauna than the brackish *Ruppia*-dominated communities (except in the Baltic). According to this diversity, the *Zannichellia*-communities resemble freshwater communities. The number of species is generally higher than in the *Ruppia*-communities and often in the same order of magnitude as in freshwater. The number of specimens is lower than in the *Ruppia* communities but significantly higher than in many freshwater communities. The maximum biomass of the *Zannichellia* stands is about the same as in *Ruppia* stands but somewhat lower than in freshwater ecosystems and much lower than in *Zostera* communities.

INTRODUCTION

This part of the study, concerning the ecology of a *Zannichellia*-dominated ecosystem, deals with the field observations in western Europe. The autecological data, presented in Part I (Van Vierssen, 1982a), will be used to see to what extent they contribute to the understanding of the distribution of the *Zannichellia* taxa. Therefore, the distribution of these taxa will be discussed in relation to a number of environmental factors such as the chlorinity of the water and its fluctuations, the substrate, water depth and climatic conditions.

A classification based on the macrophyte species and the animal species will be made. The aim is to compare the community types distinguished and to see whether these types coincide or differ. It is expected that the results of these comparisons will provide information about the relationships between the macrophytes and the animals inhabiting these stands. Comparison of the community types containing *Zannichellia* taxa with those containing *Ruppia* taxa as given by Verhoeven (1980a) may throw some light on the question of the species minimum in brackish waters, since the structural characteristics of the phytocoenoses with *Ruppia* and *Zannichellia* taxa seem rather similar. To compare the quantitative characteristics of the different *Zannichellia*-dominated phytocoenoses the biomass of the plants and animals will be studied from a northern locality (Tvärminne, Finland), some localities in The Netherlands and from a southern habitat (Camargue, France). Further, these data

will be used to quantify possible differences between the *Zannichellia*- and the neighbouring *Ruppia*-dominated communities.

The final goal of this research is the indication of the main factors causing the characteristics of communities with *Zannichellia* taxa.

DISTRIBUTION OF *ZANNICHELLIA* TAXA IN RELATION TO ENVIRONMENTAL FACTORS

Chlorinity

As was discussed by Van Vierssen (1982a), the chlorinity of the water has different impacts on the *Zannichellia* taxa when cultured. In the laboratory experiments *Z. pedunculata* Rchb. dominates *Z. palustris* L. under conditions of relatively small chlorinity fluctuations, whereas a more stable chlorinity does not lead to dominance. When studying the distribution patterns in nature, it is seen that in northern Europe (Finland) *Z. palustris*, *Z. pedunculata* and *Z. major* Boenn. are distributed in brackish waters. As Luther (1951b) described, the *Zannichellia* taxa grow to some degree in mixed stands under relatively stable chlorinity conditions (±3‰ in summer). In contrast to *Z. palustris*, the distribution of *Z. pedunculata* is limited by the chlorinity of the water. Under freshwater conditions this taxon does not grow in these latitudes and *Z. major* is restricted to the more saline areas with chlorinities exceeding 2.5‰. This species exhibits a rather low tolerance to freshwater. As a consequence of climatic and geographic conditions, the large brackish Baltic habitat is characterized by relatively stable chlorinity conditions during the growing season. However, the mean chlorinity at the entrance to the Gulf of Finland and the Bothnian Bay is higher than at the end of these two waters, although at a fixed station the chlorinity is rather stable.

Southwards, in Denmark, *Z. palustris* is no longer found at the same high chlorinities as *Z. pedunculata* and *Z. major*. Combining my own observations with those of Pedersen (1967) and Samuelsson (1934), the following chlorinity tolerances can be given for the different *Zannichellia* taxa. *Zannichellia palustris* is distributed in freshwater and in brackish waters with summer chlorinities up to ±4‰. *Zannichellia pedunculata* occurs in water with summer chlorinities between ±0.5—±8.5‰. *Zannichellia major* is restricted to a chlorinity range of ±4—±11‰.

An almost perfect separation with respect to the chlorinity ranges inhabited can be observed in The Netherlands. Many coastal habitats have a rather unstable chlorinity regime, due to their small size, shallowness, isolated position and evaporation. In the non-isolated or semi-isolated ditches, present on a very large scale in The Netherlands, the influence of the sea on the chlorinity of a part of these ditches is achieved by different mechanisms. In winter, when large quantities of rainwater have to be sluiced into the sea, the chlorinity is lowered considerably. As a consequence these habitats then often

exhibit a freshwater character, whereas in summer, when the water stays in the ditches much longer, the chlorinity of these waters increases by evaporation, airborne salt and seepage. Because of the presence of large deltas and polders below sea level, the transition between the sea and freshwater occupies a rather large area.

Zannichellia palustris is restricted to freshwater (<0.3‰ Cl^-), whereas *Z. pedunculata* is found in habitats with chlorinities between ±0.4—±7‰. This taxon is mostly found in coastal waters with a chlorinity during the growing season of less than 1‰ (more than 70% of the recorded stations), but more than 0.4‰. *Zannichellia major* almost certainly no longer occurs in The Netherlands.

In Fig. 1, the distribution of *Z. palustris*, *Z. pedunculata* and *Z. major* in The Netherlands as established by means of herbarium material (Leiden, The Netherlands) is visualized. Many of the records given in this figure date from before the closure of the Zuiderzee (see arrow, Fig. 1D) and of the estuaries in the south-western part of The Netherlands. In Fig. 1D the influence of the sea, indicated by the chlorinity of the groundwater, is illustrated. This survey was made some 20 years after the closure of the Zuiderzee (1932), by which time this sea inlet had become a freshwater lake. As is illustrated in Fig. 1A, *Z. pedunculata* is restricted to the brackish coastal zone, in contrast to *Z. palustris* which is more or less restricted to inland and/or freshwater localities. It should be noted that *Z. major* used to be present in The Netherlands. It was recorded many times along the coast of the former Zuiderzee (Fig. 1C) before its closure. At that time this sea inlet resembled to a very large extent the brackish fjords found in Denmark. The locality with *Z. major* in the south-western part of The Netherlands probably originated from a brackish creek before it disappeared due to land reclamation.

Further south in western Europe (France, southern parts of W. Germany, Switzerland), *Z. palustris* is restricted to freshwater (e.g., the Lake of Geneva, Lachavanne and Wattenhofer, 1975). *Z. pedunculata* occurs in waters with summer chlorinities between ±0.5—10‰. The chlorinity data concerning this taxon were collected in the Camargue and partly supplied by B. Britton from the Tour du Valat Foundation (Camargue). More than 60% of the habitats with *Z. pedunculata* show chlorinities lower than 2‰.

In this area many of the numerous brackish habitats dry out in summer because of the strong evaporation. A number of habitats in which salts have accumulated over a long period show very high chlorinities in summer. Verhoeven (1975, 1979, 1980a) found *Ruppia* in habitats with summer chlorinities up to ±45‰. *Zannichellia pedunculata* is obviously not as salt-tolerant and is restricted to less saline environments. *Zannichellia major* does not occur in these southern latitudes.

Geographical separation of Zannichellia *taxa*

As earlier discussed by Van Vierssen (1982a), *Z. pedunculata* dominates

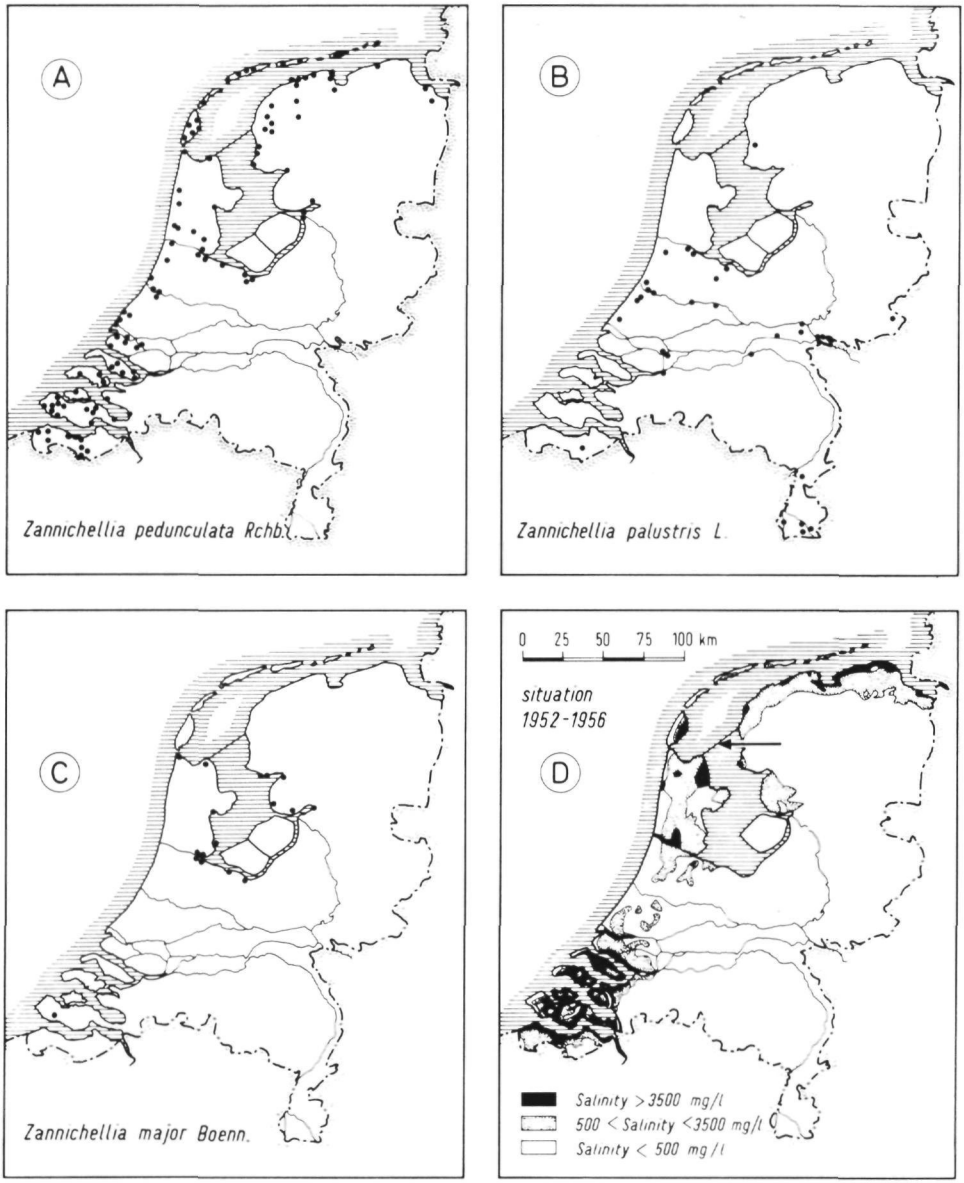


Fig. 1. Distribution of *Zannichellia* taxa in relation to salinity (‰) in The Netherlands (herbarium material from Leiden, The Netherlands).

Z. palustris when they are grown together under experimental conditions with rather small chlorinity fluctuations. Under stable chlorinity conditions no clear dominance can be observed. These results explain the existence of mixed stands of *Z. palustris* and *Z. pedunculata* in the Baltic and the Gulf of Finland. In southern latitudes, the character of the brackish habitats be-

comes more unstable, resulting in separated *Zannichellia* stands. In Fig. 2 the distribution of the three *Zannichellia* taxa with respect to the summer chlorinity and the geographical latitude in western Europe is given.

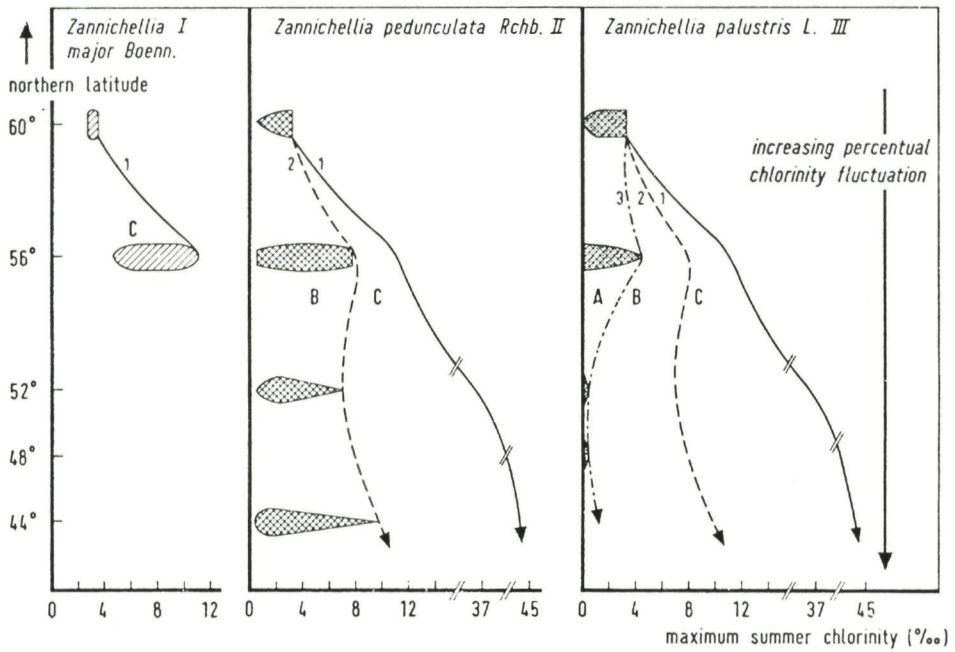


Fig. 2. Chlorinity tolerance of *Zannichellia* taxa in different European latitudes. Line 1 indicates the maximum chlorinity normally found in the latitudes indicated. The tolerance limit of *Zannichellia major* coincides with this line. Line 2 indicates the tolerance limit of *Z. pedunculata*. Line 3 indicates the tolerance limit of *Z. palustris*. The areas A, B and C indicate different community types with aquatic macrophytes in the different latitudes. For further explanation see text.

Figure 2(I) shows the distribution of *Z. major*. Line 1 indicates the maximum chlorinity normally found in the latitudes indicated. *Zannichellia major* is obviously found in the most saline waters in these northern latitudes. Within the chlorinity range of area C, this taxon occurs in mixed coenoses with other salt-tolerant species such as *Ruppia cirrhosa* (Petagna) Grande, *Ruppia maritima* L. and *Zostera marina* L.

In Fig. 2(II), the distribution of *Zannichellia pedunculata* is given in a similar way. The chlorinity tolerance of *Z. pedunculata* seems to increase towards southern latitudes but this effect is probably due to the absence of environments with the same chlorinity in northern latitudes, as indicated by line 1. As can be seen the number of habitats (indicated as area C) with chlorinities between the maximum tolerance of *Z. pedunculata* and the maximum chlorinities found increases to the south. Different aquatic plant communities from this type of habitat were described by Verhoeven (1975, 1979,

1980a). *Zannichellia pedunculata* grows together with other macrophytes as schematized to the left of line 2, in area B. As can be seen in Fig. 2(III), this species is only found with *Z. palustris* in northern latitudes. As the percentual chlorinity fluctuation increases (going to the south), *Z. palustris* becomes more restricted to pure freshwaters by the mechanisms discussed earlier. Line 3 represents the chlorinity tolerance of *Z. palustris*. In the habitats represented by area A, this taxon can be found in mixed stands together with numerous freshwater species.

Desiccation

The distribution patterns of the different *Zannichellia* taxa are determined also by the capacity to survive desiccation. In the very shallow parts of the littoral zone, desiccation may occur on a small scale. In small, temporary habitats such as isolated pools, the desiccation may be of a rather severe character. In Table I (see also section above), the number of permanent or temporary habitats in which the different taxa are recorded is given. It is obvious from this that *Z. major* is only distributed in permanent waters. As was indicated in Part I of this study (Van Vierssen, 1982a), and as will be discussed in another section, the seed production of this taxon is not very abundant and the horizontal runners, in this case the rhizome parts, are probably not very drought-resistant. Of the two subspecies of *Z. palustris* only the ssp. *repens* (Boenn.) Koch occurs in the Baltic. It is not subject to severe desiccation because in the summer the water-level fluctuations in many of its habitats are moderate. Short periods of desiccation occur but can be survived by the rhizome parts (Luther, 1951a). In Denmark *Z. palustris* ssp. *repens* is found in a relatively large number of freshwater habitats. In freshwater other aquatic macrophytes are also potential colonizers (no Cl^- master factor) and *Z. palustris* ssp. *repens* can only develop well in the very shallow parts of the littoral zone, where the water is only 1 cm or 2 cm deep and other species would be damaged because they lack morphological adaptations. These border environments can dry out, but this situation was not very frequently encountered. The seeds of *Z. palustris* ssp. *repens* also proved to be drought-

TABLE I

Number of temporary and permanent habitats with *Zannichellia* taxa studied in western Europe

	Zannichellia palustris		*Zannichellia pedunculata*		*Zannichellia major*	
	Temporary	Permanent	Temporary	Permanent	Temporary	Permanent
Finland/ Denmark	1	9	4	7	0	5
The Netherlands	2	5	43	152	—	—
France (Camargue)	—	—	27	29	—	—

resistant, but extensive desiccation experiments were not carried out with seeds of this taxon, because other more decisive factors proved to be of major importance.

Zannichellia pedunculata was found in coastal, saline areas in the Baltic area. In more southerly latitudes, a large number of habitats inhabited by this taxon dry up in summer due to the isolated character of the waters and the climatic conditions. Unlike *Z. major*, *Z. pedunculata* has the advantage of drought-resistant seeds. As was earlier discussed (Van Vierssen, 1982a), the germination of newly produced *Z. pedunculata* seeds is retarded and often inhibited by the rising chlorinity as a consequence of evaporation. This mechanism has to be considered as favourable in desiccating habitats because it prevents a loss of seedlings.

Wave action and water depth

In northern latitudes *Z. palustris* ssp. *repens* is found at a large range of depths; it may be near the water edge, embedded in the substrate or caught up in algae under a film of water which is often only several mm thick, but also at depths of more than one metre. The small specimens are rather tolerant with respect to disturbances caused by currents and wave action. In Lith (The Netherlands), *Z. palustris* ssp. *repens* is found in similar, very shallow habitats. In Lake Constance (W. Germany), apart from the very shallow areas, the water to a depth of 1.85 m was full of *Z. palustris* ssp. *palustris* specimens of more than one metre in length.

In Fig. 3 the size of *Z. pedunculata* habitats in The Netherlands is illustrated. The lower depth ranges are well represented; this is due to the fact that the brackish habitats to which this species is restricted are very small and shallow.

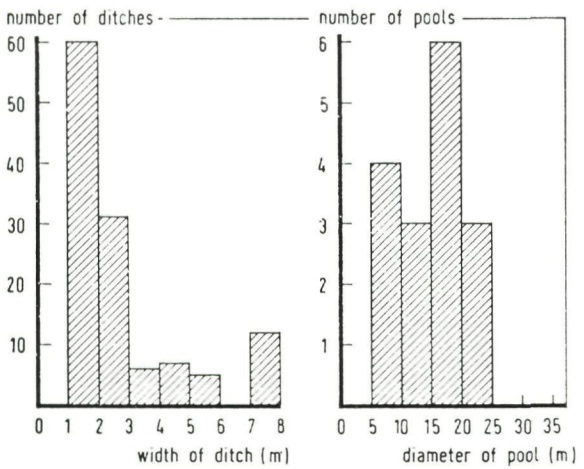


Fig. 3. Distribution of *Zannichellia pedunculata* over different size classes of ditches and pools in The Netherlands.

Because of the shallowness of the majority of the environments, zonation caused by a depth-related distribution could not be studied. However, information relevant to this was obtained from the littoral zone of the Gulf of Finland and the larger fjords in Denmark. There, *Z. pedunculata* develops in relatively deep waters in sheltered situations. A good example of this type of habitat is a sheltered bay near Jungshoved (Denmark) where large, well-developed *Z. pedunculata* specimens are found at depths of more than one metre. The distribution at greater depths is not only related to increasing hydrostatic pressure, but often also to stronger wave action and currents.

Zannichellia major, a very robust species, inhabits the deeper coastal parts of the Baltic where there is much wave action and conditions are dynamic (currents). When summarizing the affinities to wave action and depth, it can be stated that while *Z. major* inhabits the deepest parts of the environments and needs much water circulation and currents, *Z. pedunculata* often inhabits the deeper parts when these are situated in sheltered places.

Zannichellia palustris ssp. *palustris* is only widespread in large lakes and running water. This taxon can also colonize deeper parts of littoral zones, whereas *Z. palustris* ssp. *repens* is more frequently found in shallow border environments.

It has to be realized that the recorded depth distribution could also be the result of life-cycle characteristics. Perennial species such as *Z. major* are of course more frequently found in the deeper waters of environments where the shallower parts dry out frequently. In contrast to this phenomenon, annual species such as *Z. palustris* ssp. *repens*, with abundant seed production, can easily withstand temporary desiccation if their seeds are drought-resistant. In such instances, the species can be found in shallow water. In deeper parts, temperatures are too low in spring for germination to take place (the optimum temperature for germination is relatively high; 24°C). Later in the year germination occurs because temperature rises, but then the competition with other species is probably fatal at these depths.

Stagnant or running waters

When discussing the distribution of *Zannichellia* taxa with respect to these environmental factors, it has to be realized that the result of such a study is influenced by the separated distribution of these habitat types.

Zannichellia palustris was often found in running fresh water. As Haslam (1976) also describes, the growth-form of this species enables it to anchor firmly in the substrate. The material discussed earlier from the Mühlbach (West Germany; see Van Vierssen, 1982a), which was used for morphological description, produced relatively small shoots at relatively short intervals on the rhizome parts.

Zannichellia pedunculata was never observed in running water, on the one hand as a consequence of the fact that running brackish water is not often found and on the other hand as a consequence of its morphological charac-

teristics. As was pointed out earlier (Van Vierssen, 1982a) this taxon is characterized by relatively long shoots at relatively long intervals on the rhizomes, and this is not very advantageous for withstanding currents.

Substrate

Under field conditions *Z. major* is found exclusively on sandy substrates. The general impression is that this species is limited to environments with a high rate of water circulation, which guarantees a good and rapid gas exchange. The failure to cultivate this taxon on a sandy substrate also points in this direction. As water turbulence coincides with absence of silt deposits it is obvious why this species is not found on clay.

As was tested in experiments (Van Vierssen, 1982a), *Z. pedunculata* as well as *Z. palustris* develops better on substrates with a relatively high clay content. In contrast to these experiments, *Z. palustris* was observed to colonize sandy substrates in the Baltic waters. It is very likely that the amount of dissolved gasses present in these waters was more favourable than in the laboratory cultures. The general tendency of *Z. palustris* to increase its production when eutrophication occurs is striking. In Lake Constance (W. Germany) and the Lake of Geneva this phenomenon was observed by Lang (1973) and by Lachavanne and Wattenhofer (1975) respectively. This phenomenon was also observed in Scotland (Jupp and Spence, 1977). Increasing eutrophication causes an enlarged deposition of seston, resulting in an enrichment of the substrate. The observed development of *Z. palustris* at the mouth of small rivers which discharge into lakes such as Lake Constance often coincides with the presence of such deposits.

Zannichellia pedunculata is usually found on clay substrates and only in a few instances on sandy ones, because in the areas with brackish waters all bottoms are of clay.

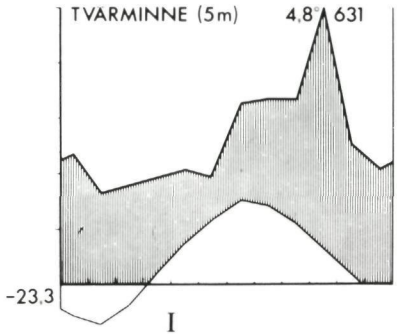
Temperature

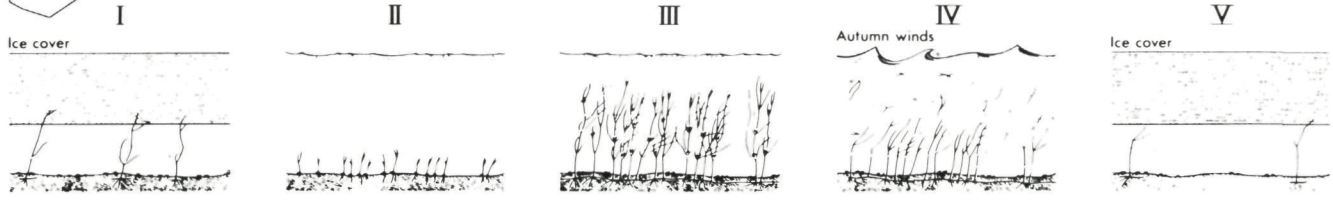
As has been stated, *Z. pedunculata* is less frequently found than *Z. palustris* in the northernmost localities. In The Netherlands the situation is reversed. This is probably due to factors other than the absence of suitable habitats. When studying the germination ecology of *Z. pedunculata* and *Z. palustris*, it is striking that the seeds of *Z. palustris* need a stratification period of about two months at 4°C, whereas the seeds of *Z. pedunculata* (and *Z. major*) germinate without delay when brought under moist conditions. This physiological phenomenon contributes to the understanding of the distribution of *Z. palustris*, which is restricted to northern and central Europe, where the necessary temperature requirements are fulfilled.

Life-cycle of Zannichellia *taxa under field conditions*

As was discussed in the previous sections, the distribution patterns of the *Zannichellia* taxa are different. In Figs. 4 and 5 the life-cycle of *Z. palustris* and *Z. pedunculata* are given for characteristic field situations. In the case of

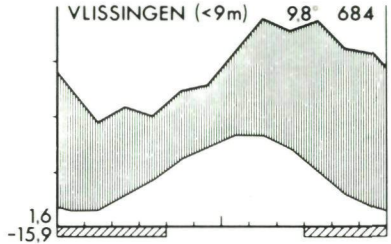
LIFE-CYCLE OF Zannichellia palustris L. (Tvärminne, FINLAND)



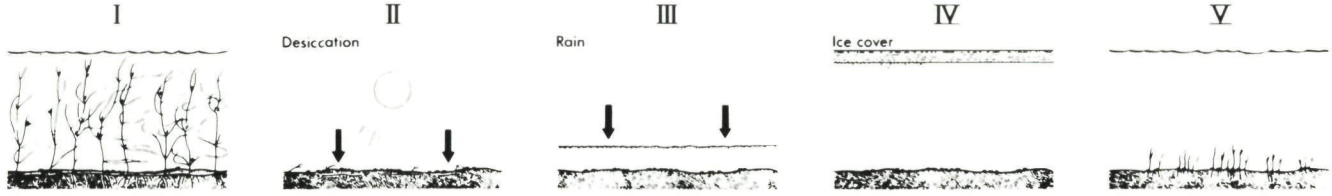


	I	II	III	IV	V
Season:	April	May	June/September	October	December/April
Water T:	$< 4°C$	$\pm 7°C$	$\pm 15°C - \pm 20°C$	$\pm 7°C$	$< 4°C$
Phenomena:	– Hibernating seeds – Stratification	– Rather low chlorinity as a result of melted snow – Rising water – Increase of daylength * Germination of seeds	– Flowering and fructifying plants – Deposition of seeds – No germination	– Loosening plant material by autumn winds – Hibernation of seeds	– Ice cover – Temporary conservation of plant material
Cause:	– Low T	* Stratification period > 2 months ($T \leq 4°C$)	* No stratification period		

Fig. 4. Life-cycle of *Zannichellia palustris* in a bay near Tvärminne (Finland).



LIFE-CYCLE OF Zannichellia pedunculata Rchb. (THE NETHERLANDS) IN TEMPORARY HABITATS



	I	II	III	IV	V
Season:	June	July/August	September/October	January	April
Water T:	± 14°C	± 17°C → 25°C	± 12°C	< 4°C	± 8°C
Phenomena:	– Flowering and fructifying plants – Deposition of seeds – Slow desiccation * Inhibited seed germination	– Desiccation – Dying of plants * Seeds under dry conditions without being damaged	– Refilling of environment with rainwater – Relatively low water T – Shortening of day-length * No seed germination	– No germination – Stratification	– Rising temperature – Relatively poor light conditions * First germination of seeds
Cause:	* Rising chlorinity by evaporation * Rising temperature * Relatively dark conditions underneath aquatic macrophytes	* Drought-resistance of seeds	* Retarded germination under poor light conditions * Relatively high optimum T requested for germination		* Stratification period causes germination at relatively poor light conditions * Lowered optimum germination temperature

Fig. 5. Life-cycle of *Zannichellia pedunculata* in a temporary habitat in The Netherlands.

Z. palustris (ssp. *repens*), a vegetation in the Gulf of Finland has been chosen as an example. The life-cycle of *Z. palustris* (Fig. 4) is given in relation to the environmental conditions as relevant in the different periods of the year. In spring, when ice and snow melt, *Z. palustris* seeds have spent several months under cold conditions, which is necessary to induce germination. As was found earlier (Van Vierssen, 1982a), germination occurs best in freshwater which is frequently present then as a result of freshwater runoff from the land and river discharge (Luther, 1951a,b). The germination experiments with *Z. palustris* (ssp. *repens* and ssp. *palustris*) seeds show that dark conditions are insufficiently stimulating to induce germination. The relatively long days in this latitude contribute to a rather good germination in May at relatively low temperatures. By June a rich vegetation has developed and the first flowering and fructifying plants can be observed. Deposited seeds are prevented from germinating as the temperatures are too high for stratification. In autumn the winds loosen the old plants, the temperature falls and the seeds are subjected to the cold period necessary to produce seedlings next spring.

In Lake Constance (W. Germany) *Z. palustris* (ssp. *palustris*) is probably perennial in the deeper parts (Lang, 1967).

In Fig. 5 the life-cycle of *Z. pedunculata* as found in a characteristic temporary habitat is illustrated. The situation as given is frequently found in pools in the coastal zone. A general description of this type of habitat in The Netherlands is given by Van Vierssen and Verhoeven (1982). The results of the germination experiments with *Z. pedunculata* seeds by Van Vierssen (1982a) clearly contribute to the understanding of the mechanisms involved in the successful maintenance of this species in this type of environment.

As a starting point in Fig. 5, the presence of a luxuriant *Z. pedunculata* vegetation in summer has been chosen. From the middle of May flowering and fructifying plants occur. Ripe seeds are deposited underneath the dense *Zannichellia* vegetation (Fig. 5(I)). The germination of the seeds is prevented by the low light intensity under this plant mass, as was found in germination experiments. These non-stratified seeds do not germinate under dark conditions. Another factor preventing germination is the sometimes high temperature of the rather shallow waters in high summer. In these isolated, small, temporary water, the chlorinity increases during summer and in the outer zones, as the edge of the water withdraws, the chlorinity will reach high maxima just before desiccation occurs. These two factors also slow down or inhibit germination. As is obvious, these prevailing factors ensure that the seeds survive the approaching dry period (Fig. 5(II)). Desiccation does not damage the seeds. When the habitats are refilled with rainwater, the seeds germinate. The relatively low temperatures and relatively poor light conditions prevent germination in autumn (Fig. 5(III)), but after the cold winter months they germinate in March and April at low light intensities (Figs. 5(IV) and (V)). Van Vierssen (1982a) showed that *Z. pedunculata* seeds germinated under dark conditions after a stratification period (at 4°C) of two months.

An interesting result with a significant ecological meaning was the observed lowering of the optimum germination temperature after stratifica-

tion. The optimum temperature in freshwater under dark conditions (in spring, the daylight conditions are relatively poor and the chlorinity decreased by relatively large amounts of rainwater) is 16°C. At higher chlorinities the optimum germination temperature is even lowered to 12°C. Of course some seeds do germinate in summer, but die because of the inevitable desiccation. When desiccation is not complete, mature plants live on and can survive the winter, sometimes underneath an ice cover. It was observed that when the ice disappeared, a rapid decomposition of the bulk of the material followed.

Many plants appear to be perennial. In many freshwater habitats, where desiccation does not play an important ecological role, the presence of *Z. pedunculata* is largely influenced by the presence of other macrophytes. When Nymphaeids (e.g., *Potamogeton natans* L.) or *Hydrocharis morsus-ranae* L. develop, the light conditions are very poor underneath the floating leaves and unfavourable for *Z. pedunculata*. In the brackish habitats where competition between parvopotamids occurs, *Z. pedunculata* can also be replaced by other macrophytes during the growing season. To facilitate a quick discharge of polder water in the winter, this plant material is supposed to be removed from the ditches at the end of the summer or in the autumn. As the seeds of *Z. pedunculata* germinate at relatively low temperatures its seedlings are usually able to develop freely the following spring before the macrophytic competitors restart their growth.

In the Camargue (France), where *Z. pedunculata* is frequently co-dominant with *Ranunculus baudotii* Godr., more than one *Z. pedunculata* generation can be observed in one year. After the first seedlings have grown into a vegetation, many habitats dry out. When the summer or autumn rains refill these environments, the temperature is still high enough to produce a second generation from the deposited seeds of the first generation. *Zannichellia major* plants have been observed to survive the winter underneath the ice cover in the Gulf of Finland (H. Luther, 1979, personal communication). These plants develop in spring, but produce fruits in late summer. The seed-setting of this species is significantly less luxuriant and occurs later in the season than in *Z. palustris* and *Z. pedunculata*. In the life-cycle of *Z. major*, seeds and seed-germination do not play a very important role.

Discussion

The use of autecological experiments to explain observations made in the field proved successful in elucidating the distribution patterns. The overall distribution patterns in Europe are clearly influenced by the germination ecology of the different taxa. The seeds of *Z. palustris* need a stratification period of several months. This explains the observed distribution pattern in which *Z. palustris* is dominantly distributed in northern latitudes or more continental localities. Recently, however, *Zannichellia* material from a coastal locality from Greece (kindly supplied by H. Huijbregts) was shown to have $2n = 24$ chromosomes and looked very similar to the *Z. palustris* ssp. *palustris*

material from western Europe. It is not known whether the local climatic conditions provide a stratification period or not. The fact that there may be intraspecific differences in the germination ecology of *Z. palustris* cannot be excluded. McMillan (1978, 1979) and McMillan and Phillips (1979) found intraspecific differences in sea-grass populations. Important observations with respect to the germination ecology of seeds from different European localities were made by Thompson (1968, 1970a, 1970b). This author found different optimum germination temperatures for different species of Caryophyllaceae related to the geographical latitude and their climatic conditions. However, some intraspecific variation was not excluded. Thompson's results and those from the autecological experiments with *Zannichellia* seeds (Van Vierssen, 1982a) show similarities.

The chlorinity-tolerance experiments show that the tolerance limits of the plants are determined to a great extent by the way in which they are subjected to these chlorinities. The heterogeneity of the habitats in western Europe with respect to chlorinity obviously increases when going from north to south. At the latitudes of the Netherlands, the separation of the *Z. palustris* and *Z. pedunculata* populations with respect to the chlorinity factor has become complete. The reason for this separation can be partly understood from competition experiments carried out with *Z. palustris* and *Z. pedunculata*.

The restriction of *Z. major* to the Baltic waters can be partly explained from its life-cycle characteristics. The obligate halophilous character of this species is obvious. Its absence in southern latitudes, where there is a lack of habitats with a chlorinity regime suitable for this species, is therefore not surprising.

DISTINCTION OF COMMUNITIES WITH *ZANNICHELLIA* TAXA

Introduction

In this section a survey will be made of the species composition of phytocoenoses with *Zannichellia* taxa as they occur in western Europe. Below (p. 118) a number of community types are distinguished on faunistic grounds.

The phytosociological method has been used to describe the community types in this section. After the discussion on the community types with *Zannichellia* taxa, some general thoughts concerning phytosociological classifications will be given. In spite of a number of objections, reference will be made to the phytosociological syntaxa with *Zannichellia* taxa as given in the literature, because most of the available information on the co-existence with other species at community level is presented by means of relevés and syntaxa according to the Zürich—Montpellier School.

The most important and representative phytosociological syntaxa as found in the literature are summarized in Table IX. It is obvious that this survey is only a very small selection of the very numerous syntaxa which can be found in the literature. The taxonomical and nomenclatural problems involved with

the *Zannichellia* material from western Europe have clearly influenced the distinction of well-defined syntaxa.

In The Netherlands, where *Z pedunculata* occurs in inland coastal waters, den Hartog (1958) distinguished a Potameto-Zannichellietum pedicellatae. The stands consisted of *Potamogeton pectinatus*, *Z pedunculata*, *Chara canescens* Desv. & Lois , *Chara vulgaris* L and some *Ruppia maritima* specimens, which were found in the slightly brackish waters of the Balgzandkanaal Den Hartog (1963) presented a Callitricho-Ranunculetum baudotii with *Callitriche obtusangula* Le Gall and *Ranunculus baudotii* Godr as character species *Zannichellia pedunculata* reaches its optimum development in this association. These brackish habitats were characterized by fluctuating chlorinities and desiccation in summer. Verhoeven (1980a) distinguished a Ruppietum brevirostris in the Mediterranean area with a subassociation Zannichellietosum pedicellatae in mesohaline, extremely shallow marshes, drying out early in summer (mean salinity below 5‰ Cl) An extensive study of brackish-water phytocoenoses was carried out by Lindner (1978) in the southern Baltic (Boddenketten). *Zannichellia pedunculata* (sub nomine *Z palustris* ssp *pedicellata* (Wahlenb & Rosen) Arcang) is presented as a character species of the Ruppion order. *Zannichellia major* (sub nomine *Z palustris* ssp *palustris* var *polycarpa Prahl*) is said to be locally present in the Ruppietum spiralis Iversen 1934 Koch (1926) described a Parvopotameto-Zannichellietum tenuis association for fresh, shallow waters which dry out in winter (Switzerland). According to Lang (1967), who studied the aquatic macrophyte communities in the littoral zone of Lake Constance, one of the character species of this association is *Z palustris* ssp. *repens* Lang (1967) also pointed out that the Najadetum marinae (Oberdorfer 1957) Fukarek 1961, with *Najas marina* L as a character species, is identical with the Parvopotameto-Zannichellietum tenuis Koch 1926. Species such as *Najas flexilis* (Willd) Rostk. & Schmidt and *Najas minor* All. are said to be restricted to this association. *Z. palustris* spp. *palustris* was described by Baumann (1911) from localities where rivers discharge into Lake Constance The association with this taxon was called Zannichellietum palustris Besides *Z palustris* ssp. *palustris* as a character species, *Potamogeton pectinatus* and *Potamogeton pusillus* (sub nomine *Potamogeton panormitanus* Biv) and sometimes *Chara contraria* Kutz were present. Lang (1973) re-examined this association but then distinguished two types, a Zannichellietum typicum under eutrophic conditions and a Zannichellietum sparganietosum in fast-running shallow waters with rather high nutrient loads. Differential species are *Myriophyllum spicatum* L., *Potamogeton nodosus* Poir. and *Sparganium erectum* ssp. *neglectum* (Beeby) Sch. & Thell. After re-examination of the *Najas* species, this author proposed the name Najadetum intermediae for the communities with *Najas*, earlier named Najadetum marinae (Oberdorfer, 1957) Fukarek 1961. This latter association was characterized by *Najas marina*, whereas the vegetation in Lake Constance was characterized by *Najas intermedia* (= *N marina* var. *intermedia* (Wolfgang) A. Br.). The Najadetum intermediae is treated as

being identical with the Parvopotameto-Zannichellietum tenuis (Lang, 1973). The different types distinguished within this association are based on the trophic level, the Najadetum potametosum pusilli (= Najadetum potametosum panormitani) indicates slightly eutrophic conditions, whereas the Najadetum typicum is characteristic for the oligo- and mesotrophic shallow littoral zones.

The situation as discussed for Lake Constance can be considered to be representative of the situation encountered in more lakes in central Europe (e.g., Lake Geneva). Oberdorfer (1977) summarized the associations as found in the southern part of West Germany. Besides the Najadetum intermediae (Koch, 1926) Lang 1973 and the Zannichellietum palustris ssp palustris Lang 1967, this author distinguishes a Ranunculo-Sietum erecto-submersi (Roll 1939). Th. Muller 1962 with *Z palustris* ssp *repens* as a differential species. This association is characteristic for fast-running waters rich in calcium and up to 1.50 m deep. *Zannichellia palustris* ssp *repens* is also dealt with as a differential species for the Callitrichetum obtusangulae Seibert 1962, abundant in eutrophic, moderate to fast-running water Further observations of associations in running water were made by Kohler et al. (1971). They distinguished a Ranunculo-Sietum with *Ranunculus fluitans* Lam., *Ranunculus fluitans* × *trichophyllus* and *Z palustris* ssp *repens* as differential species. Many intermediate types between the Callitrichetum obtusangulae and this association were found. Grube (1975) studied running waters in Niedersachsen (W. Germany) and found *Z palustris* associated with *Ranunculus fluitans*, *Callitriche platycarpa* Kutz. and *Potamogeton crispus* L. in small streams, eutrophicated by sewage. In more than 50% of the relevés *Z palustris* was accompanied by *Callitriche platycarpa*

Westhoff and den Held (1969) discussed the Najadetum marinae with respect to the situation in The Netherlands. They considered this association as characteristic for oligohaline small lakes or broads with water-level fluctuations. The Parvopotameto-Zannichellietum palustris is not considered indigenous in The Netherlands because the differential species *Najas minor* and *Najas flexilis* are absent.

Because of the confusion of *Z major* Boenn with *Z palustris* ssp. *palustris* in western Europe (Lang, 1973 indicated that these two taxa are identical), freshwater communities with *Z palustris* ssp. *palustris* can be found under the name Zannichellietum majoris (Baum. 1911) Lang 1967 in the literature (Meriaux, 1978). The name of this syntaxon is very confusing and should therefore be rejected.

Methods

The description of the species composition of the communities with *Zannichellia* taxa in western Europe was made by means of the methods developed by the Zurich—Montpellier School. The releves made at the different stations were arranged separately for the different areas visited The abundance of the various species was recorded by means of a modified Braun-

Blanquet scale (Barkman et al., 1964) The syntaxa as given in the literature will be compared with the community types as distinguished in the next section (Table IX).

Results

The phytocoenoses distinguished were selected on a basis of dominant environmental factors, the macrophyte species composition and their life-strategies.

In general, three categories of communities with *Zannichellia* taxa can be distinguished, communities in brackish water, communities in stagnant freshwater, and communities in running freshwater. These three types will be discussed in the next sections.

Brackish water

(A1) Communities with *Z palustris* ssp *repens* on sandy substrates along (wind) exposed shores of the Baltic with relatively constant summer chlorinities of 2.5—3 5‰ Accompanying aquatic macrophytes in the shallower parts are *Potamogeton filiformis* Pers., *Ruppia maritima* var *brevirostris* (Agardh) Aschers & Graebn., whereas in the deeper parts this *Zannichellia* taxon is accompanied by the more robust *Potamogeton pectinatus Chara aspera* Detharding ex Willdenow frequently occurs in this community. In Fig. 6A, the general characteristics of a habitat with this type of community are illustrated (releves 1—5, Table II).

(A2) Communities with *Z major* in water more than 50 cm deep, or along exposed shores on sandy substrates in the Baltic A good water circulation is important. The summer chlorinities are rather constant (2 5—3 5‰) *Zannichellia major* is frequently accompanied by *Potamogeton pectinatus, Zostera marina, Ruppia cirrhosa* and *Potamogeton filiformis* The distribution of *Ruppia cirrhosa* and *Zannichellia major* in the deeper outer parts of the Baltic is probably due to the perennial character of these plants (relevés 6—8, Table II).

(A3) Communities in shallow, sheltered bays in the Baltic with moderate wave action and with the less frequently encountered *Z pedunculata* as a characteristic accompanying species of *Z palustris* ssp *repens*. *Potamogeton pectinatus* and *Potamogeton filiformis* This community occurs under relatively stable chlorinity conditions (2.5—3.5‰, relevés 9—11, Table II).

In Denmark the spatial separation of the *Z palustris* ssp *repens* and *Z pedunculata* populations was observed In the brackish fjords the *Zannichellia* taxa are found in the oligo- to mesohaline range The physical geography and climatic conditions are such that in summer more brackish habitats dry out than in northern latitudes.

(A4) Communities with *Zannichellia major, Zannichellia pedunculata, Zostera marina, Potamogeton pectinatus, Ruppia maritima* var *maritima* and *Ruppia cirrhosa* in permanent waters with a chlorinity exceeding 4.5‰ in


A


B


C

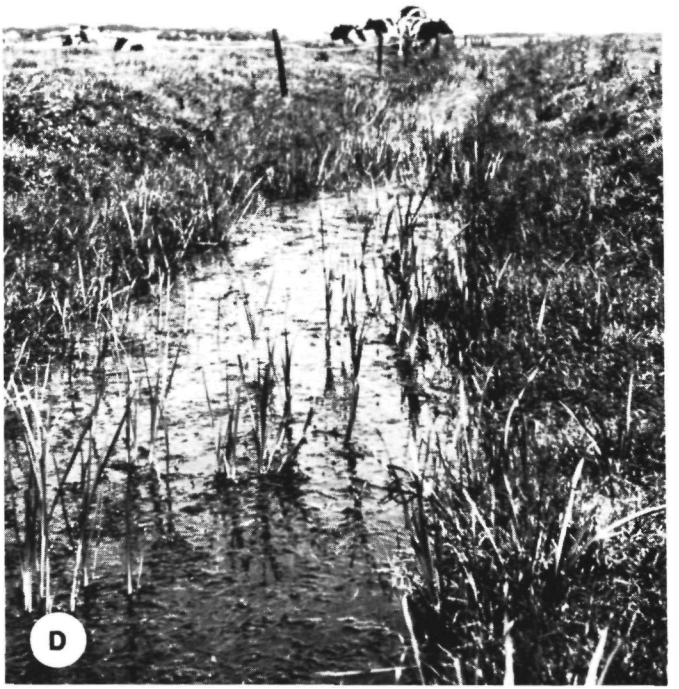

D

Fig. 6. Characteristic habitats with *Zannichellia* taxa in western Europe. A, community with *Z. palustris* ssp. *repens*, Gulf of Finland, Tvärminne, Finland. B, community with *Z. pedunculata*, temporary habitat, Salin de Giraud, Camargue, France. C, community with *Z. palustris* ssp. *palustris*, littoral zone, Lake Constance, West Germany. D, community with *Z. pedunculata*, ditch, Terschelling, The Netherlands. E, community with *Z. pedunculata*, pool, Terschelling, The Netherlands. F, community with *Z. palustris* ssp. *repens*, running water, Skals Å, Denmark.

TABLE II

Survey of *Zannichellia* relevés from Tvärminne (Finland) (August, 1979)

Locality:	1	2	3	4	5	6	7	8	9	10	11
Substrate:	e	e	c(org)	e	d	e	e	e	e	d	d(org)
Chlorinity (‰):	±3.3	3.3	3.3	3.3	3.3	3.3	3.3	3.3	3.3	3.3	3.3
Zannichellia palustris ssp. *repens* (Boenn.) Koch	1	2a	2b	2a	1	—	+	—	1	2b	2b
Potamogeton filiformis Pers.	2b	1	1	1	—	1	1	1	1	+	—
Potamogeton pectinatus L.	—	+	—	1	1	2a	1	1	—	+	1
Chara aspera Detharding ex. Willdenow	2a	2b	—	2b	—	+	—	—	+	+	2b
Ruppia maritima var. *brevirostris* (Agardh.) Aschers. Graebn.	+	+	3	2a	—	1	—	—	—	2b	2b
Zannichellia major Boenn.	+	—	—	—	—	1	1	1	—	—	—
Zostera marina L.	—	—	—	—	—	1	—	1	—	—	—
Zannichellia pedunculata Rchb.	—	—	—	—	—	—	—	—	2b	+	+
Chara tomentosa L.	—	—	2a	—	—	—	—	—	—	—	—
Chorda filum (L.) Stackh.	—	—	—	1	1	—	—	—	—	—	—
Zannichellia palustris × *pedunculata*	—	—	—	—	—	—	—	—	1	—	—
Ruppia maritima L. var. *maritima*	—	—	—	—	—	—	—	—	—	+	—
Najas marina L.	—	—	—	—	—	—	—	—	—	—	1
Chara canescens Desv. et Lois. in Lois.	—	—	—	—	—	—	—	—	—	—	1
Myriophyllum spicatum L.	—	—	—	—	—	—	—	—	—	—	r
Ruppia cirrhosa (Petagna) Grande	—	—	—	—	—	1	—	—	—	—	—
Ranunculus baudotii Godr.	—	—	—	—	—	—	—	r	—	—	—
Fucus vesiculosus L.	—	—	—	—	1	—	—	—	—	—	—

Substrates: c(org) = clay with high organic content, d = sandy clay, e = sand

TABLE III

Survey of *Zannichellia* relevés from Denmark (July, 1979)

Locality:	1	2	3	4	5	6	7	8
Substrate:	d	e	e	e	e	d(org)	e	d(org)
Chlorinity (‰):	4.9	6.2	6.2	2.9	0.3	3.1	3.1	0.8
Zostera marina L.	1	2a	—	—	—	—	—	—
Ulva lactuca L.	1	—	—	—	—	—	—	—
Zannichellia major Boenn.	1	1	1	—	—	—	—	—
Ruppia maritima L. var. *maritima*	—	+	2	—	—	—	—	—
Ruppia cirrhosa (Petagna) Grande	1	—	1	—	—	—	—	—
Potamogeton pectinatus L.	—	+	1	—	—	1	+	—
Potamogeton pusillus L.	—	—	—	3	—	2b	+	1
Zannichellia pedunculata Rchb.	—	—	4	2	1	2a	—	—
Zannichellia palustris ssp. *repens* (Boenn.) Koch	—	—	—	—	—	1	1	3
Zannichellia palustris × *pedunculata*	—	—	—	—	—	+	—	+
Myriophyllum spicatum L.	—	—	—	1	—	—	+	—
Ceratophyllum demersum L.	—	—	—	—	—	—	1	—
Enteromorpha spec.	1	—	—	—	—	+	—	—
Tolypella glomerata (Desv. in Lois.) Leonh.	—	1	—	—	—	—	—	—
Chara canescens Desv. et Lois. in Lois	—	—	2m	—	—	—	—	—

Substrates: d = sandy clay, d(org) = sandy clay with high organic content, e = sand, e(org) = sand with high organic content.
Localities: 1 Mariager Fjord, 2 Prestø Fjord, 3 Prestø Fjord, 4 Ringkøbing Fjord, 5 Stavreby, Jungshoved (pool), 6 Ringkøbing Fjord, 7 Ringkøbing Fjord, 8 Hjarbaek Fjord.

summer and with moderate chlorinity fluctuations. This community type is frequently encountered in Danish fjords (relevés 1—3, Table III).

(A5) Communities with *Z. pedunculata*, *Potamogeton pectinatus*, *Potamogeton pusillus* L. (sometimes *Z. palustris* ssp. *repens*) in semi-permanent waters with chlorinities of less than 3.5‰ in summer, e.g. shallow parts of Danish fjords (relevés 4—8, Table III).

In The Netherlands the brackish communities were investigated in three areas: the Ilperveld, the northern part of The Netherlands and the area with the supralittoral pools as described by Van Vierssen and Verhoeven (1982). The characteristic phytocoenoses as found can be described as follows.

(A6) Communities with *Ruppia maritima* var. *maritima*, *Z. pedunculata* and *Potamogeton pectinatus* in semi-isolated permanent waters such as canals and ditches. The chlorinities fluctuate with maxima ranging from 5—6‰, a fluctuation within one year of ca. 4‰, resulting in a mean chlorinity of ca. 3—3.5‰ (this does not apply to the Ilperveld, but *Ruppia* is only a relict there). This community type occurs in the coastal zone of The Netherlands and in northern Germany (F.R.G., 1979, personal observation). For the characteristic chlorinity régime see Fig. 7A,B (relevés 1—3, Table IV; 1—3, Table V).

(A7) Communities with *Zannichellia pedunculata*, *Potamogeton pusillus*

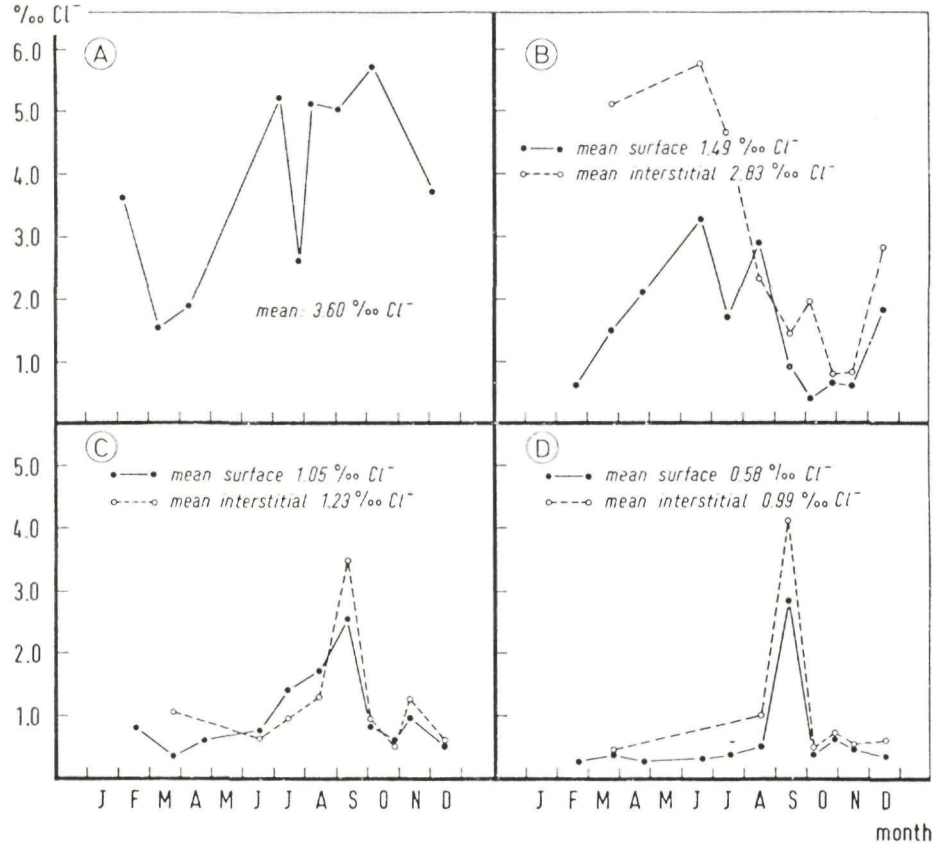


Fig. 7. Chlorinity regimes of habitats with *Z. pedunculata* in The Netherlands. A, Zeeuws-Vlaanderen (community type A6). B, ditch, Terschelling (community type A6). C, ditch, Terschelling (community type A7). D, ditch, Terschelling (community type A7).

and *Potamogeton pectinatus* in semi-isolated permanent waters such as canals and ditches with fluctuating chlorinities. The floating vegetation layer consists of *Lemna gibba/Lemna minor*, *Lemna trisulca* L. and sometimes (in autumn) *Azolla filiculoides* Lam. The maximum chlorinities range from 0.60—5.00‰, with fluctuations within one year from 0.70 up to ca. 4.0‰, resulting in mean chlorinities from 0.30 up to 3.00‰. For the characteristic chlorinity regime see Fig. 7C,D. The community probably has a wide distribution in the coastal zone of The Netherlands and in northern Germany (F.R.G., 1979, personal observation). The general appearance of this widely distributed habitat is illustrated in Fig. 6D (relevés 4—11, Table IV; 4,5, Table V; 1—26, Table VI).

(A8) Communities with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Potamogeton pusillus*, *Ranunculus baudotii*, *Callitriche obtusangula* and *Myriophyllum spicatum* in semi-isolated habitats such as canals, ditches and

TABLE IV

Survey of *Zannichellia* relevés from the Ilperveld (The Netherlands, August, 1977)

Locality:	1	2	3	4	5	6	7	8	9	10	11
Depth (cm):	15	15	15	15	15	20	10	20	20	15	15
Substrate:	a	a	a	a	a	a	a	a	a	a	a
Chlorinity (‰):	0.51	0.47	0.45	0.30	0.56	0.57	0.48	0.42	0.47	0.50	0.43
Category:	A	A	A	B	B	B	B	B	B	B	B
Ruppia maritima L. var. *maritima*	5	2a	1	—	—	—	—	—	—	—	—
Zannichellia pedunculata Rchb.	4	1	3	3	4	3	3	4	3	3	2b
Potamogeton pectinatus L.	2	—	1	—	—	1	1	2b	1	1	2b
Potamogeton pusillus L.	—	—	—	3	3	2b	+	+	+	—	+
Najas marina L.	—	—	2b	—	—	—	—	—	—	—	—
Ceratophyllum demersum L.	+	—	—	—	—	—	—	—	—	—	—
Myriophyllum spicatum L.	+	—	—	—	—	—	—	—	—	—	—
Lemna gibba L.	+	1	—	2a	—	1	+	1	2b	+	—
Lemna trisulca L.	—	—	+	2a	—	—	—	—	—	—	—
Azolla filiculoides Lam.	—	1	—	—	—	1	1	1	1	∴	3

Category A: fluctuating chlorinities with a maximum of 3‰, mean chlorinities 0.40—0.60‰.
Category B: fluctuating chlorinities with a maximum of 0.60‰ and mean chlorinities of 0.45‰.
Substrate category: a = peat.

TABLE V

Survey of *Zannichellia* relevés from Terschelling (The Netherlands, July, August, 1978)

Locality:	1+	2	3	4	5
Substrate:	c	c	c	d	d
Chlorinity (‰)	5.12	3.40	0.80	0.70	0.50
Category:	A	A	B	B	B
Ruppia maritima L. var. *maritima*	2a	3	+	—	—
Zannichellia pedunculata Rchb.	3	2a	2b	3	3
Potamogeton pectinatus L.	2b	—	1	1	1
Potamogeton pusillus L.	—	1	—	2a	2a
Ceratophyllum demersum L.	—	+	—	+	—
Lemna gibba L.	—	1	—	1	+
Lemna trisulca L.	—	—	+	+	—
Spirodela polyrhiza (L.) Schleid.	—	—	—	+	—
Enteromorpha spec.	—	1	1	+	—
Vaucheria dichotoma	—	—	—	5	—

Category A: mean annual chlorinity between 2.8—3.6‰. Maxima 5.1—5.7‰. Minima 0.70—1.50‰ Cl^-.
Category B: mean annual chlorinity 0.85—1.00‰. Maxima 1.5—4.1‰ Cl^-. Minima 0.35—0.45‰ Cl^-.
Substrates: c = clay, d = sandy clay.
+ = pool, Zeeuws-Vlaanderen, The Netherlands.

sometimes pools that temporarily and partly dry up. They are found in the coastal zone of The Netherlands and northern Germany (F.R.G., 1979, personal observation). The floating vegetation layer consists of *Lemna gibba/Lemna minor* and *Lemna trisulca*. The mean summer chlorinities are ca. 0.55‰. Two variants of this community type can be distinguished, a variant with *Callitriche* species in habitats that dry up regularly and a variant with *Myriophyllum spicatum* L. in habitats that dry up less often (relevés 27—57, Table VI).

(A9) Communities with *Zannichellia pedunculata*, *Ranunculus baudotii* and *Potamogeton pectinatus* in isolated pools with maximum summer chlorinities of ca. 3.00‰ (June—September) that temporarily and partly dry up. The minimum summer chlorinities are ca. 0.7‰. The distribution of this type of habitat is largely determined by landscape, land use and climatic conditions and it can be found in the northern part of West Germany and in the coastal zone of The Netherlands, Belgium and France. The habitat type of categories 8 and 9 is illustrated in Fig. 6E (for relevés see Van Vierssen and Verhoeven, 1982).

The local distribution of *Z. pedunculata* in The Netherlands as found in the communities described above is illustrated in Figs. 8 and 9. As is obvious from Fig. 8 this taxon and therefore the communities described also, has a strictly coastal distribution. *Z. pedunculata* also occurs in other coastal areas in The Netherlands where the chlorinities of the inland waters are suitable

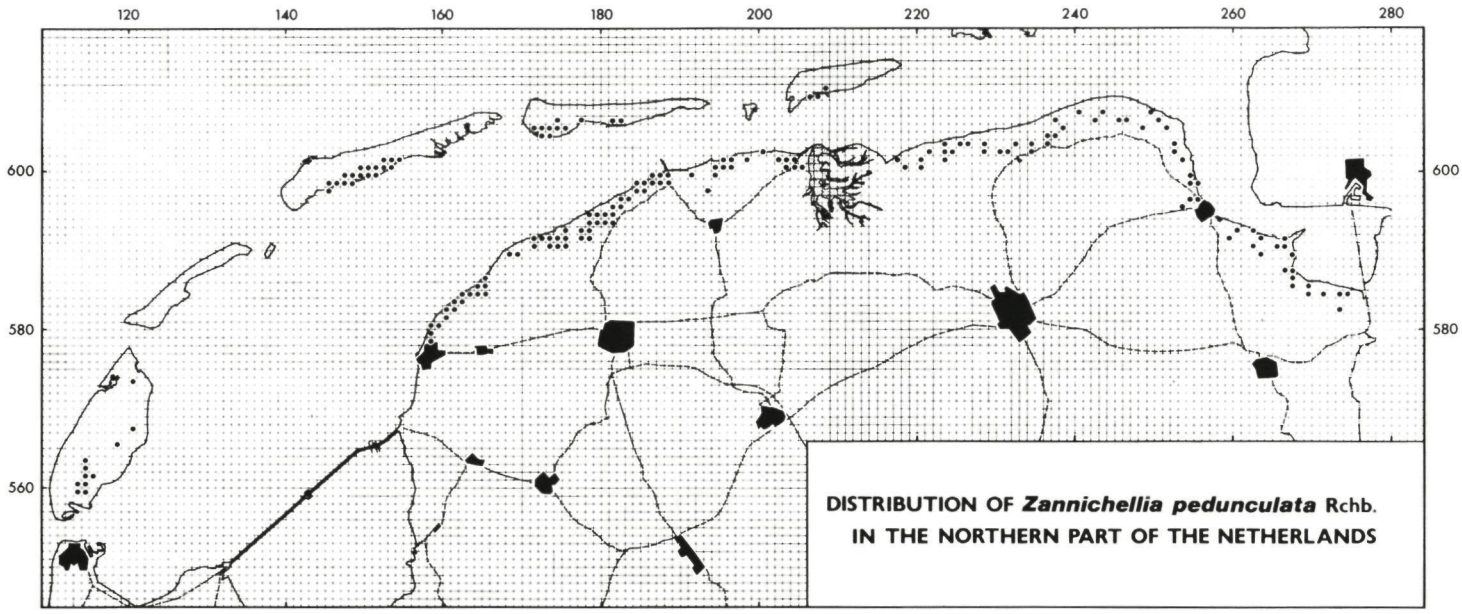


Fig. 8. Distribution of communities with *Z. pedunculata* in the northern part of The Netherlands.

TABLE VI

Survey of *Zannichellia* relevés in the northern part of The Netherlands

Locality	1	2	3	4	5	6	7	8	9
Date (1979)	7-8	7-8	21-8	22-8	7-8	28-8	18-7	28-8	28-8
Depth (cm)	60	70	100	40	35	50	30	60	50
Zannichellia pedunculata Rchb.	4	3	3	2b	5	4	4	3	1
Potamogeton pectinatus L.	3	1	3	2b	3	—	2b	1	1
Potamogeton pusillus L.	2a	2a	3	2b	2a	1	1	—	—
Ranunculus baudotii Godr.									
Myriophyllum spicatum L.									
Callitriche obtusangula le Gall									
Potamogeton natans L.									
Ceratophyllum demersum L.									
Ceratophyllum submersum L.									
Chara spec.									
Elodea nuttallii (Planch.) St. John									
Potamogeton crispus L.									
Lemna gibba/minor L.	3	3	2a	2b	1	1	1	3	3
Lemna trisulca L.	2b	1	1	2a	1	1	—	2a	4

Locality	19	20	21	22	23	24	25	26	27
Date (1979)	6-7	3-7	10-7	17-7	11-7	11-7	17-7	10-7	26-6
Depth (cm)	40	125	50	80	50	50	60	10	30
Zannichellia pedunculata	2b	2a	2a	1	1	1	1	4	3
Potamogeton pectinatus	2b	1	3	4	3	3	2a	—	—
Potamogeton pusillus	—	—	—	2a	1	—	—	—	2b
Ranunculus baudotii							—	—	1
Myriophyllum spicatum							—	—	—
Callitriche obtusangula									
Potamogeton natans									
Ceratophyllum demersum									
Ceratophyllum submersum									
Chara spec.									1
Elodea nuttallii									
Potamogeton crispus									
Lemna gibba/minor							1	1	2a
Lemna trisulca							—	—	2b

Locality	37	38	39	40	41	42	43	44	45
Date (1979)	29-8	10-7	10-7	6-7	17-7	4-7	21-8	11-7	6-7
Depth (cm)	30	100	40	100	50	60	20	35	40
Zannichellia pedunculata	3	—	3	1	1	—	5	—	—
Potamogeton pectinatus	3	—	2b	—	—	1	—	—	—
Potamogeton pusillus	—	3	—	2a	—	2a	—	1	3
Ranunculus baudotii	—	2a	1	—	5	1	1	1	—
Myriophyllum spicatum	2a	2a	2b	1	—	—	—	—	—
Callitriche obtusangula		1	3	1	4	1	1	1	2a
Potamogeton natans		2b	1	—					
Ceratophyllum demersum		—	—	—					
Ceratophyllum submersum		2a	—	—					
Chara spec.		—	2a	—					
Elodea nuttallii	2a	—	—	—					
Potamogeton crispus									
Lemna gibba/minor	3	—	—	2a	—	4	1	2b	—
Lemna trisulca	2a	2a	—	—	1	2a	—	3	—

10	11	12	13	14	15	16	17	18
21-8	26-6	18-7	27-6	29-8	29-8	18-7	7-8	10-7
80	20	40	30	35	25	20	30	40
5	5	4	3	3	3	3	2b	1
1	1	—	—	2b	3	3	—	3
—	—	—	2a	—	—	—	—	3

2b	1	1	2b	1	1	1	3	1
—	—	1	3	—	—	—	3	—

28	29	30	31	32	33	34	35	36
7-6	26-6	27-6	21-8	4-7	10-7	10-7	6-7	6-7
20	100	25	30	5	40	100	100	35
4	3	4	4	4	1	2a	2a	2b
—	—	—	—	—	1	1	2b	4
1	2b	—	—	—	—	2b	4	—
1	1	1	2a	1	3	1	—	—
—	—	—	—	—	—	2a	1	2a

2a	—	1	1	—	1	2b	—	1
—	2b	1	—	—	1	1	—	2a

46	47	48	49	50	51	52	53	54	55	56	57
29-8	26-6	6-7	6-7	11-7	17-7	11-7	7-8	18-7	18-7	21-8	6-6
20	35	35	50	40	100	50	100	60	50	50	40
2b	3	—	—	2b	1	—	2a	3	3	4	2a
—	—	—	—	—	2b	2b	2a	—	—	1	—
—	—	5	—	—	2a	—	—	4	1	—	3
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
2a	3	1	1	1	—	1	—	1	2b	1	2a
			4	3	2a	—	—	—	—	—	—
								2a	2a	—	—
		1									
							1	—	—		
							1	1	2a		
1	—	—	—	—	2a	1	1	2b	3	2b	2a
—	—	—	2a	—	1	—	—	1	—	1	—

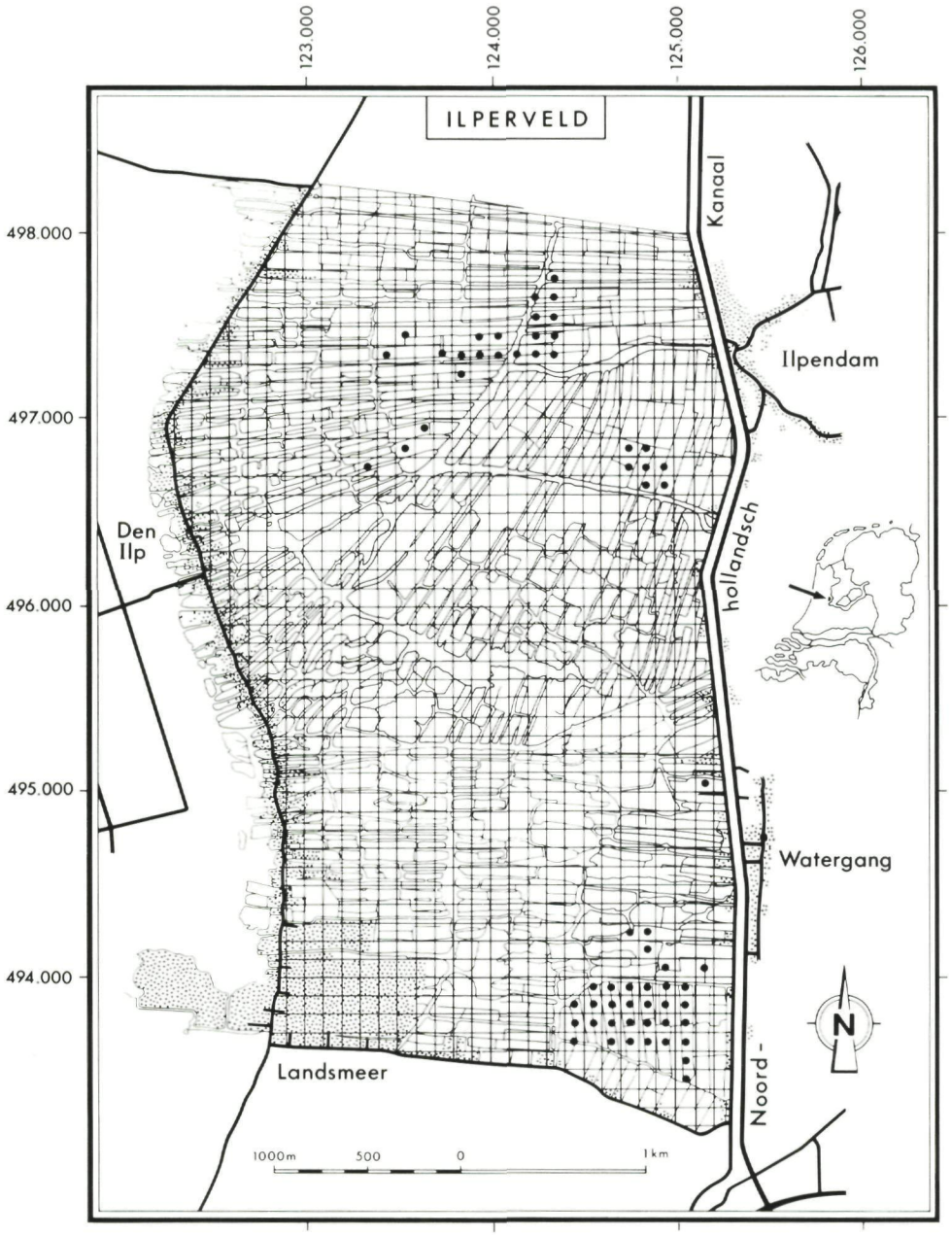


Fig. 9. Distribution of communities with *Z. pedunculata* in the Ilperveld, The Netherlands.

but these areas were not studied extensively. The inland distribution of *Z. pedunculata* as given in Fig. 9 originates from the time when the Zuiderzee still existed and salt seepage caused relatively high chlorinities in this area. The chlorinities are still relatively high because of the salts that remained in the bottom of the sediments. The chlorinities are continuously

decreasing, however, and these brackish-water communities will probably disappear soon.

In southern Europe the situation in the Camargue was studied. In Table VII a survey of phytocoenoses with *Z. pedunculata* in brackish waters is presented. The original data for this table were kindly supplied by B. Britton of the Tour du Valat Foundation (Camargue, France). Several patterns of co-existence of aquatic macrophytes can be observed. Desiccation is of great importance, particularly in combination with the chlorinities reached during the growing season. Seven communities could be distinguished on the basis of these qualitative data. The most important and widely distributed communities are summarized under A10 and A11. Although no identification on the species level was carried out with respect to *Zannichellia*, the greater part of the material must have been *Z. pedunculata*. *Zannichellia peltata* Bertol. was found only once (C. den Hartog, 1980, personal communication).

(A10) Communities with *Zannichellia pedunculata*, *Potamogeton pectinatus* and *Chara* species such as *Chara aspera* and *Chara canescens*. Occasionally a floating vegetation with *Lemna gibba*, *Lemna minor*, and *Azolla filiculoides** was found. The mean summer chlorinity is ca. 5.5‰. As shown in Fig. 10, a large number of these habitats dry out (1—7, Table VII).

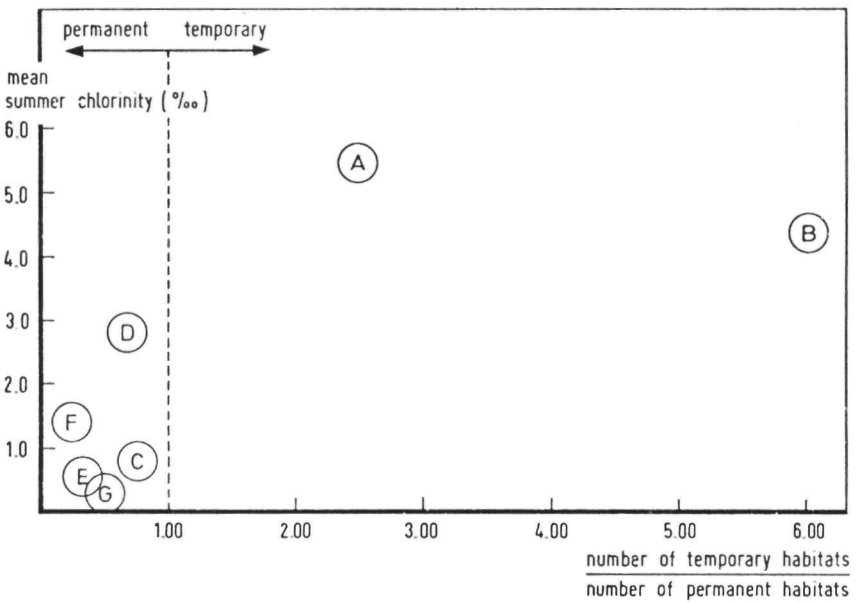


Fig. 10. Occurrence of community types with *Z. pedunculata* in relation to the mean summer chlorinity (‰) and the level of permanency of habitats in the Camargue (France). A, community type A10. B, community type A11. C, community type A12. D, community type A13. E, community type A14. F, community type A15. G, community type A16.

*The original data mentioned *Azolla caroliniana* Willd. When visiting the Camargue, the author only found *Azolla filiculoides*. Therefore this taxon is mentioned here. This applies to the community types A10—A16.

TABLE VII

Survey of phytocoenoses with *Zannichellia pedunculata* in the Camargue (France)

Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Zannichellia pedunculata Rchb.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Potamogeton pectinatus L.		+			+	+		+		+	+	+	+	+		+
Chara species		+	+	+	+		+	+				+	+	+	+	
Ranunculus baudotii Godr.								+	+	+	+	+	+	+	+	+
Myriophyllum spicatum L.																
Potamogeton pusillus L.																
Ceratophyllum demersum L.																
Utricularia australis R. Br.																
Ruppia spec.																
Najas minor All.																
Potamogeton nodosus Poir.																
Hydrocharis morsus-ranae L.																
Potamogeton natans L.																
Potamogeton crispus L.																
Potamogeton lucens L.																
Lemna minor L.		+			+		+								+	+
Azolla filiculoides Lam*.						+	+									
Lemna trisulca L.															+	+
Lemna gibba L.		+				+		+								

A

Mean chlorinity: 5.5‰
Temporary / Permanent = 2.5

B

Mean chlorinity: 4.4‰
Temporary / Permanent = 6.0

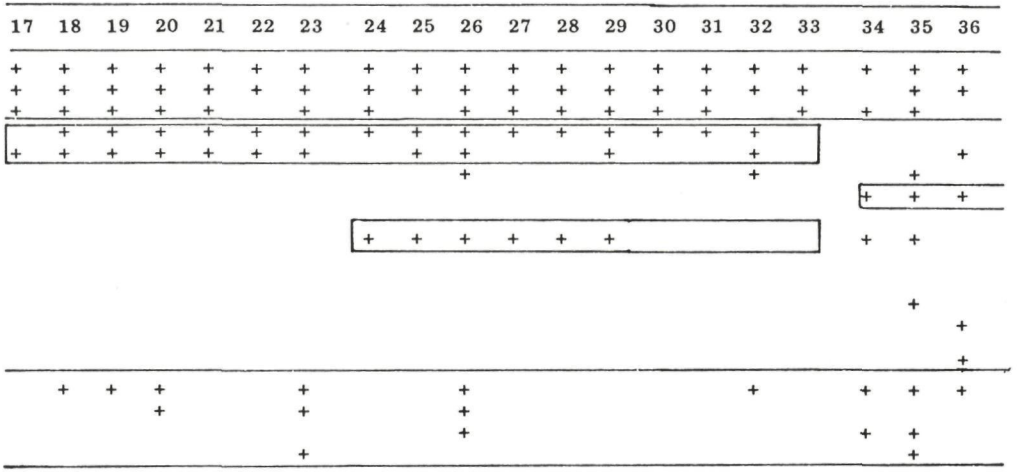
Locality	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Zannichellia pedunculata Rchb.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Potamogeton pectinatus L.	+	+	+		+	+	+		+	+	+	+	+	+	+	+	+	+	
Chara species	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Ranunculus baudotii Godr.																			
Myriophyllum spicatum L.																			
Potamogeton pusillus L.			+		+	+	+		+	+	+	+	+	+	+				+
Ceratophyllum demersum L.					+	+	+		+				+	+					
Utricularia australis R. Br.					+						+	+	+	+				+	
Ruppia spec.	+	+	+	+	+	+													
Najas minor All.												+	+	+	+	+	+	+	+
Potamogeton nodosus Poir.							+	+	+			+		+	+				
Hydrocharis morsus-ranae L.						+	+			+	+	+	+	+					
Potamogeton natans L.	+																		
Potamogeton crispus L.						+													
Potamogeton lucens L.																			
Lemna minor L.	+	+	+		+	+		+	+	+	+	+	+		+			+	+
Azolla filiculoides Lam*.					+		+	+	+	+									
Lemna trisulca L.										+		+	+						
Lemna gibba L.										+			+						

F

Mean chlorinity: 1.40‰
Temporary / Permanent = 0.25

G

Mean chlorinity: 0.23‰
Temporary = 0.50
Permanent



C

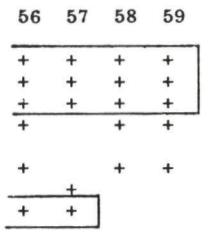
Mean chlorinity:
0.80‰
Temporary
Permanent = 0.75

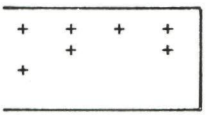
D

Mean chlorinity:
2.80‰
Temporary
Permanent = 0.66

E

Mean chlorinity:
0.53‰
Temporary
Permanent = 0.33





*The original data mentioned *Azolla caroliniana* Willd. When visiting the Camargue, the author only found *Azolla filiculoides* Lam. Therefore this taxon is mentioned here.

(11B) Communities with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Chara* species such as *Chara aspera* and *Chara contraria* and *Ranunculus baudotii*. The floating vegetation (when present) consists of *Lemna minor* and *Lemna trisulca* L. (and probably also *Lemna gibba*). The mean summer chlorinity is ca. 4.4‰, which is rather lower than the chlorinity found in community type A10 (see also Fig. 10). The desiccation rates are somewhat higher in this community. Structurally they very much resemble the communities discussed under 9 and the life-strategies (drought-resistant seeds, land-forms) are similar. This type of community can be found from the coastal areas in The Netherlands to southern Europe. An illustration of the habitat characteristics for the Camargue is given in Fig. 6B (8—16, Table VII).

(12C) Communities of a more permanent character with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Chara* species, *Ranunculus baudotii*

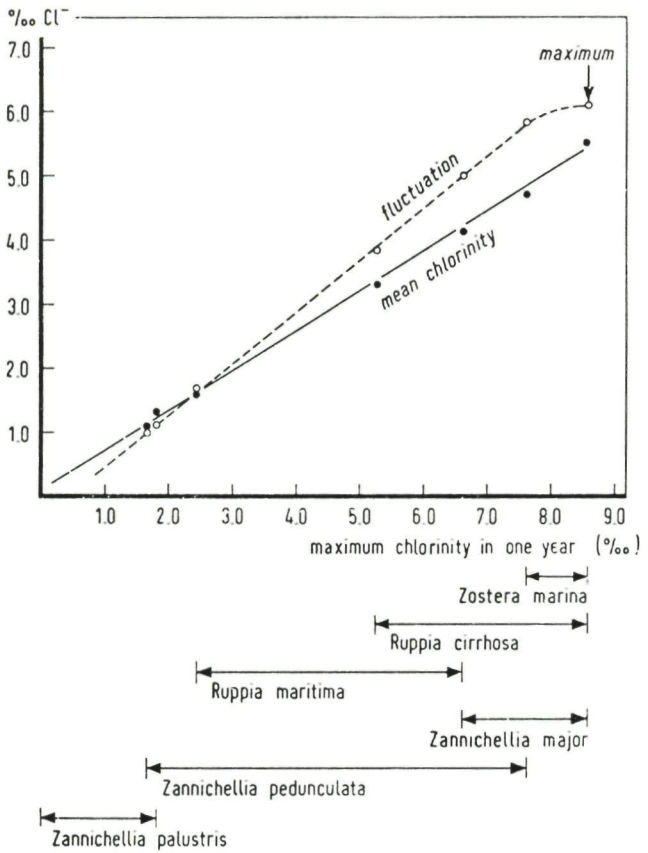


Fig. 11. Chlorinity tolerance of aquatic macrophytes and the relationships between the maximum chlorinity in one year and the fluctuation of the chlorinity, and the mean chlorinity in habitats in a Baltic Bay (data from Lindner, 1978).

and *Myriophyllum spicatum*. The floating vegetation consists of *Lemna minor*, *Lemna trisulca* and *Azolla filiculoides**. A minority of the sampling stations dried out sometimes. There is a clear structural resemblance to community type 8 (17—23, Table VII).

(13D) Communities of a more permanent character with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Chara* species, *Ranunculus baudotii*, *Myriophyllum spicatum* and *Ruppia*. The floating vegetation consists of *Lemna minor*, *Lemna trisulca* and *Azolla filiculoides**. The mean summer chlorinity is 2.8‰ (24—33, Table VII).

(14E) Communities with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Chara* species and *Ceratophyllum demersum* L. The floating vegetation (when present) consists of *Lemna minor*, *Lemna gibba*, *Lemna trisulca* and *Azolla filiculoides**. The mean summer chlorinity is 0.53‰ and the habitats are characterized by permanence in contrast to the communities summarized under 12 (34—42, Table VII).

(15F) Communities with *Zannichellia pedunculata*, *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Chara* species, *Ranunculus baudotii*, *Najas minor* All. and *Potamogeton nodosus* Poir. The mean summer chlorinity is 1.4‰. The floating vegetation (when present) consists of *Lemna minor*, *Lemna gibba*, *Lemna trisulca* and *Azolla filiculoides**. This community type is permanent (43—51, Table VII).

(16G) Communities with *Zannichellia pedunculata*, *Potamogeton pectinatus*, *Chara* species, *Ranunculus baudotii* and *Utricularia australis* R.Br. The floating vegetation (when present) consists of *Lemna minor*, *Lemna trisulca* and *Azolla filiculoides**. These freshwater habitats are characterized by relative impermanency (52—59, Table VII).

The types A10 and A11 represent the most important *Zannichellia*-dominated vegetation stands. The rest of the community types represent transitions to freshwater ecosystems.

Stagnant freshwater

In the stagnant freshwaters of western Europe *Z. palustris* is widely distributed. It is frequently found in large lakes, such as Lake Constance and Lake Geneva. As was discussed in Baumann (1911), Lang (1967) and Van Vierssen (1982a), *Z. palustris* ssp. *repens* is distributed in the very shallow border zone of freshwater pools and lakes. In Table VIII the *Z. palustris* s.l. relevés of the freshwater habitats are summarized. Very fine and fragile *Z. palustris* ssp. *repens* plants are present in very shallow water during a short period of the growing season. In The Netherlands the subspecies was found in Lith in the shallowest parts of a former bed of the river Meuse together with *Potamogeton pectinatus*, *Potamogeton pusillus*, *Myriophyllum verticillatum* L., *Potamogeton perfoliatus* and *Najas marina*. In the Bisonbaai (The Netherlands), *Z. palustris* ssp. *repens* specimens were found under similar conditions but no other macrophytes were present, probably due to human influences (recreation). This taxon was found in the outer zones of

TABLE VIII

Survey of *Zannichellia palustris* relevés in western Europe (summer 1978, 1979, 1980)

Locality:	1	2	3	4	5	6	7	8
Substrate:	e	d(org)	e	d(org)	c	c	d	d
Depth (cm):	20	15	15	150	15	15	10	5
Zannichellia palustris L. ssp. *palustris*	2a	—	1	4	—	—	—	—
Zannichellia palustris ssp. *repens* (Boenn.) Koch	—	2a	—	—	1	1	1	1
Ranunculus fluitans Lam.	—	—	1	—	—	—	—	—
Potamogeton pectinatus L.	2a	2b	—	2	1	—	—	—
Myriophyllum spicatum L.	2a	—	—	—	—	—	—	—
Potamogeton crispus L.	1	+	—	—	+	—	—	—
Chara vulgaris L.	1	—	—	—	—	—	—	—
Potamogeton perfoliatus L.	—	2b	—	—	+	1	—	—
Lemna gibba L.	—	1	—	—	—	—	—	—
Enteromorpha spec.	—	+	—	—	—	—	—	—
Najas marina L.	—	—	—	—	2a	—	—	—
Myriophyllum verticillatum L.	—	—	—	—	1	—	—	—
Potamogeton lucens L.	—	—	—	—	—	1	—	—
Nymphoides peltata (Gmel.) O. Kuntze	—	—	—	—	—	2a	—	—
Nuphar lutea (L.) Sibth & Sm.	—	—	—	—	—	2a	—	—
Potamogeton pusillus L.	—	—	—	1	1	—	—	—

Localities: 1 Mühlbach, West Germany, running water; 2 Skals Å, Denmark, running water; 3 Gulp, The Netherlands, running water; 4 Lake Constance, West Germany, stagnant water; 5 Lith, The Netherlands, stagnant water; 6 Dodewaard, The Netherlands, stagnant water; 7 Bisonbaai, The Netherlands, stagnant water; 8 Klejtrup Sø, Denmark, stagnant water.
Substrates: c = clay, d(org) = sandy clay with high organic content, e = sand.

a pool near Dodewaard (The Netherlands) in a vegetation with *Potamogeton lucens* L., *Nymphoides peltata* (S.G. Gmel.) O. Kuntze, *Nuphar lutea* (L.) Sibth. & Sm. and *Potamogeton perfoliatus* (somewhat deeper parts).

A habitat almost identical with the Bisonbaai was found in Denmark (Klejtrup Sø) and the small groups of plants near the water's edge were exactly the same as the vegetation stands found in The Netherlands. Although the accompanying macrophytes (when present) include very different species, these communities are placed together in this study, partly on floristic grounds, partly on functional and structural grounds.

A group consisting of communities with *Z. palustris* ssp. *repens* in very shallow freshwaters under mesotrophic conditions is distinguished. The most important factor in the distribution of *Z. palustris* ssp. *repens* seems to be the very shallow character of the outer zones of the freshwater bodies.

(B1) Poor pioneer coenoses of *Z. palustris* ssp. *repens* lacking other macrophytes due to human influences (such as recreation), strong exposure or the very short aquatic nature of the habitat. In The Netherlands, this situation is

TABLE IX

Comparison of phytosociological names

Syntaxa in literature	This study
Parvopotameto-Zannichellietum tenuis Koch 1926	p.p.B1, p.p.B2
Najadetum marinae (Oberdorfer 1957) Fukarek 1961	p.p.B1, p.p.B2
Najadetum intermediae (Koch 1926) Lang 1973	p.p.B1, p.p.B2
a. Najadetum typicum	
b. Najadetum potametosum pusilli	
Zannichellietum palustris ssp. palustris Lang 1967	
a. Zannichellietum typicum	B4
b. Zannichellietum sparganietosum	C1
Ranunculo-Sietum erecto-submersi (Roll 1939) Th. Müller 1962	C1, p.p.C2
Callitrichetum obtusangulae Seibert 1962	C2, p.p.C1
Ruppietum brevirostris subass. zannichellietosum pedicellatae Verhoeven 1980	A10
Ruppietum maritimae subass. zannichellietosum pedicellatae Verhoeven 1980	A6
Ruppietum maritimae subass. ruppietosum brevirostris Verhoeven 1980	p.p.A1, p.p.A2
Ruppietum maritimae subass. najadetosum marinae Verhoeven 1980	p.p.A1
Ruppietum cirrhosae subass. zosteretosum marinae Verhoeven 1980	p.p.A2
Potameto-Zannichellietum pedicellatae Den Hartog 1958	A6
Callitricho-Ranunculetum baudotii Den Hartog 1963	p.p.A11, p.p.A12, p.p.A8, p.p.A9
Ranunculetum baudotii Braun—Blanquet 1952	p.p.A11, p.p.A12, p.p.A8, p.p.A9

frequently encountered when new drainage canals are constructed. This type of phytocoenosis is probably distributed all over Europe but has been overlooked because of the inconspicuous character of *Z. palustris* ssp. *repens* (relevés 7, 8, Table VIII).

(B2) Communities with *Z. palustris* ssp. *repens*, *Potamogeton pectinatus*, *P. pusillus*, sometimes *P. crispus*, *P. perfoliatus* and dominant stands of *Najas marina* in fresh, mesotrophic standing waters. The phytocoenosis is restricted to the littoral zone of relatively large waters in the depth range 0.05—0.70 m. There is some water-level fluctuation and wave action is moderate. This community is distributed throughout central Europe but is not present in the Scandinavian area (relevé 5, Table VIII).

(B3) Communities with *Z. palustris* ssp. *repens*, *P. pectinatus*, *Nymphoides peltata*, *Nuphar lutea*, *P. lucens* and *P. perfoliatus*. The temporarily dry outer zones are colonized by the small *Z. palustris* ssp. *repens* plants. The habitats in The Netherlands consist of pools originating from dike-bursts in the neighborhood of large rivers such as the Rhine, Meuse and Waal. These waters are often characterized by the presence of magnopotamids and nymphaeids. The general distribution of this community in western Europe has not been studied (relevé 6, Table VIII).

The communities in which *Z. palustris* ssp. *palustris* are distributed are characterized by greater permanency.

(B4) Communities with *Z. palustris* ssp. *palustris* (dominant stands), *P. pectinatus* and *P. pusillus* under eutrophic conditions. These communities are distributed in the deeper parts (0.50—1.80 m) of eutrophic lakes in central Europe but probably not in the coastal zone of western Europe because of the lack of suitable habitats. The abundance of these communities has been stimulated by the recent eutrophication that has taken place all over Europe (Lang, 1973; Lachavanne and Wattenhofer, 1975; Jupp and Spence, 1977). In contrast to the habitats discussed under 1, 2 and 3, this community is confined to permanent habitats (although the winter water-level is low the habitat remains wet; relevé 4, Table VIII and Fig. 6C).

Running water

As was discussed in an earlier section, *Z. palustris* occurs also in running water. It is often uncertain to which of the two subspecies the various authors are referring. The two subspecies obviously both possess certain qualities enabling them to colonize this habitat. There is no doubt that the material collected in the Skals Å (Denmark, see Table VIII) is *Z. palustris* ssp. *repens*. The specimens found in the Mühlbach (W. Germany) and the Gulp (The Netherlands) have been identified by the author as *Z. palustris* ssp. *palustris*.

(C1) Communities in running water with *Z. palustris* ssp. *palustris* accompanied by *Ranunculus fluitans*. Distributed in running water rich in calcium, often eutrophicated by human influence. The *Z. palustris* ssp. *palustris* vegetation as found in the Gulp (The Netherlands) belongs to this community type, which is probably distributed all over Europe except for the coastal zone (relevé 1, 3, Table VIII and Fig. 6F).

(C2) Calmer parts of running waters as discussed above are colonized by *Z. palustris* ssp. *palustris*, accompanied by *Callitriche obtusangula* and the other above-mentioned species Silty deposits are present as a result of the decreased stream velocity. Locally, *Potamogeton perfoliatus* and *Groenlandia densa* (L.) Fourr. are present. This community is identical with the Callitrichetum obtusangulae (Kohler, 1971, Kohler et al., 1971) and the Zannichellietum sparganietosum as described by Lang (1973).

Discussion

A comparison of the different habitats where *Zannichellia* taxa are (co-) dominant or regularly distributed show some striking phenomena. In the northern part of western Europe all the taxa are found in brackish water, although the chlorinity tolerances are different (Luther, 1951a, b, Lindner, 1978). The communities in the oligohaline and mesohaline range are characterized by mixed stands with a large number of aquatic macrophytes (including the Characeae) In northern Germany (F.R.G.) and the coastal zone of The Netherlands, the species composition is obviously poorer at similar chlorinity levels. As was earlier discussed, the differences between the environments become more obvious in these latitudes. In the discussion concerning the species minimum in brackish water, the fluctuations in salinity are considered partly responsible for this minimum (summary of this discussion given by Verhoeven, 1980a). It can be clearly seen from the phytosociological relevés that the number of aquatic macrophytes which occur in the Baltic generally exceeds that of the stands in The Netherlands. Species which occur at the same chlorinity in Tvarminne (Finland) have a rather different range in The Netherlands. The question that arises is whether this macrophyte species poverty is due to the chlorinity stress or some other factor. In Fig. 11 the relationship between the maximum chlorinity and the mean chlorinity, the relationship between the difference between the maximum and minimum chlorinity as recorded in one year and the maximum chlorinity is graphically represented The original data for this figure were taken from Lindner (1978) and adapted for this purpose. It can be seen that the chlorinity-tolerance limits of the aquatic macrophytes in this brackish area in the northern part of Germany (G D.R., Baltic) overlap The vegetation is characterized by mixed stands of a large number of macrophytes (e.g., *Ruppia* spp., *Zannichellia* spp. and *Zostera* spp.). These do not occur in mixed stands in The Netherlands. The relationships, as illustrated in Fig. 11, are of a linear character. Although a few species are not represented there, a similar situation was found in Tvarminne (Finland; Luther, 1951a, b). Figure 12 gives the same chlorinity relationships for The Netherlands.

A visual comparison of these two figures shows that the straight parts of the 'fluctuation' and 'mean' chlorinity lines have almost identical gradients. The chlorinity-tolerance boundaries of the various macrophytes coincide with those parts on the 'mean chlorinity' line where the mean chlorinity line show

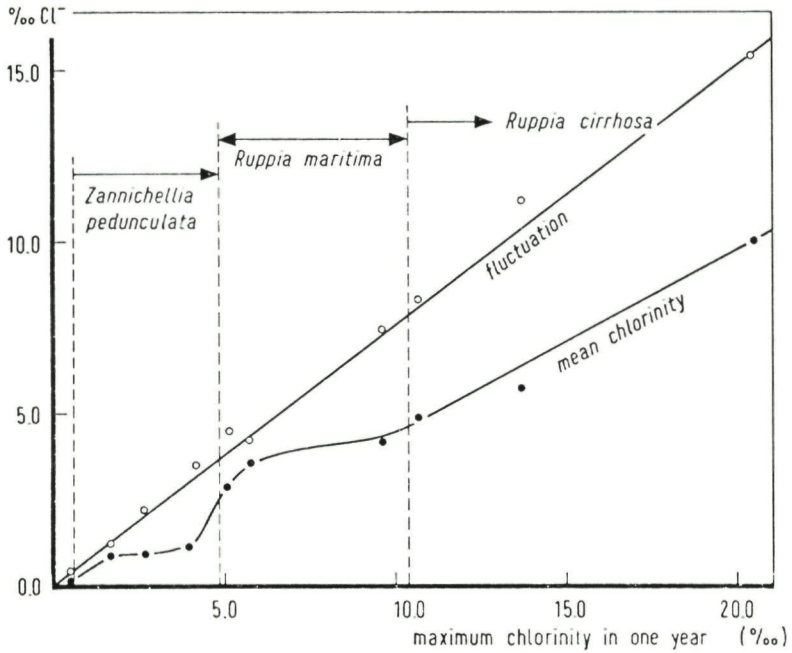


Fig. 12. Chlorinity tolerance of aquatic macrophytes and the relationship between the maximum chlorinity in one year and the fluctuation of the chlorinity, and the mean chlorinity in brackish habitats in The Netherlands.

a relatively sharp increase with respect to the maximum chlorinity. This observation probably means that it is not the chlorinity fluctuations alone which are the cause of the poorer species composition of the phytocoenoses in The Netherlands at these mean chlorinities. These characteristic relations between the various chlorinity parameters are the result of the water management (and the size of the habitat). As shown in Fig. 12, an increase of the maximum chlorinity does not always mean a proportional increase of the mean chlorinity. This is caused by the fact that, during the winter months, the superfluous polder waters are sluiced into the sea and the salt seepage is diluted by a relatively large amount of rainwater. Thus the influence of the different levels of salt seepage is balanced to a large extent. In summer, however, when little rainwater is available, so there is no superfluous freshwater, and the sluices are kept closed the different salt seepage levels become obvious. The relatively sharp increase of the mean chlorinity is caused by the relatively long period with high chlorinities in summer. Since these high chlorinities (somewhat lower than the maximum) do not influence the fluctuation of the chlorinity it is obvious that the length of such a period with relatively high chlorinities is not detectable in the 'fluctuation' curve. It seems obvious that the clear separation of the distribution patterns of the macrophytes is partly the result of these phenomena. The aquatic macrophytes are clearly affected by the

length of the period with relatively high chlorinities The impact of these phenomena on the species number will be discussed further in the section 'structural aspects of the vegetation' (p 105).

On the community level some general points have to be made to show how a complex set of processes leads to the co-existence of species and on what feeble grounds the distinction of the phyto-sociological syntaxa is based.

(1) A phytosociological approach would be more valuable if a causal approach to the origin of the co-existence in a relevé was made part of the vegetation analysis. Two identical coverage figures for one species in separate relevés could be the result of two different life-strategies under the actual environmental conditions. The long-term success of a species is clearly not only determined by its actual coverage percentage. Should vegetation stands be classified according to species composition alone or (e.g.) according to their life-strategies?

(2) When a large number of rather similar habitats with approximately the same species composition is found in a certain area, one tends to consider this group of co-existing species as a characteristic vegetation unit. The term 'characteristic' is then used in the meaning of 'most frequently encountered'. One should not forget, however, that throughout the long period of evolution many modern habitat types (frequently man-made) just did not exist. Therefore one cannot exclude the possibility that species combinations other than those now frequently found in all kinds of man-made habitats were characteristic with respect to origin and mutual relationships (when existing). Should a classification be based on historical evolutionary criteria or on the species combinations most frequently encountered nowadays?

(3) Generally two processes lead to co-existence. The first of these arises out of a species' ability to cope with the abiotic environmental conditions. A large number of species are just not able to survive high chlorinities. The second arises out of the different levels of competition. Generally co-existence means niche differentiation. As discussed above, the occurrence of a species in two different habitats can be achieved by different processes. In the Baltic area species co-exist in a permanent habitat with rather stable chlorinity conditions. It is to be expected that the survival processes there are totally different from those observed in southern Europe, where fluctuating chlorinities and desiccation play an important role. To the south, the total diversity of the habitats with respect to desiccation and chlorinity increases considerably. Different autecological abilities also offer extra chances for species in such environments. A species such as *Ruppia cirrhosa* has the advantage of a higher chlorinity tolerance than *Z. pedunculata*. *Ruppia maritima* var. *brevirostris* has the advantage of high seed production which enables it to survive long dry periods; an adaptation which the perennial *Ruppia cirrhosa* lacks. Between *Z. pedunculata* and *Ruppia maritima* var. *brevirostris* obvious differences in the length of the period to complete the life-cycle exist. *Zannichellia major* is a perennial which needs clear water, whereas *Z. pedunculata* can stand some turbidity.

The number of species capable of surviving a chlorinity stress is restricted. Every additional stress under natural conditions will exclude another species without the chance of it being replaced by another, until there are no potential colonizing species left. The advantage to a species of these different special abilities becomes apparent during natural selection by the environment. Referring to Fig. 2 it is obvious that these phenomena play an important role in southern Europe.

The classification of the *Zannichellia*-dominated communities is rather difficult. In Table IX the syntaxa with *Zannichellia* from the literature are compared with the community types distinguished in the present study. It is obvious that a number of syntaxa and community types are identical. Some differences arise from the fact that in the present study a clear distinction was made between communities with *Z. palustris* ssp. *palustris* and those with *Z. palustris* ssp. *repens*. Other differences obviously arise from the fact that Verhoeven (1980a) emphasized the importance of *Ruppia* in the communities he studied. He gives *Z. pedunculata* (sub nomine *Z. palustris* ssp. *pedicellata*) as characteristic for a subassociation whereas it also characterizes the A6 and A10 communities in the present study. Den Hartog (1981) presents a provisional hierarchical classification on a worldwide scale for poikilosaline waters.

Within the Ruppietea (J. Tüxen, 1960) emend. den Hartog and Segal 1964 he distinguished the Ruppietalia (J. Tüxen, 1960) emend. den Hartog 1981 with *Z. palustris* s.l. as a character taxon. As was discussed by Van Vierssen (1982a), this taxon actually comprises four taxa. Only two species are completely confined to brackish water; *Z. major* and *Z. pedunculata*. *Z. palustris* ssp. *palustris* communities are confined to freshwater as are the stands of *Z. palustris* ssp. *repens* in central Europe. In northern Europe the latter can be found in brackish water and is classified within the Ruppietea. In southern latitudes this taxon is only found in communities belonging to the Potametea. Further, *Z. pedunculata* is dominant in the Potameto-Zannichellietum pedicellatae den Hartog 1958 and the Callitricheto-Ranunculetum baudotii Den Hartog 1963. These two syntaxa belong to different alliances (Ruppion and Callitricho-Batrachion, respectively). This distinction is a clear result of the increase of the number of different habitats within the brackish habitat (see previous section).

The classification of the *Chara* communities also poses a problem. If they are placed in a separate class, the Charetea, it is suggested that the presence or absence of these algae is not essential for the identity and characteristics of the total phytocoenosis. However, small plants such as *Zannichellia* species in the Baltic certainly do have to cope with *Chara* species in the competition for space. Therefore, this approach does not seem very satisfying. The *Chara* stands are a very characteristic component of the brackish-water communities with *Ruppia* and *Zannichellia* taxa.

It can be concluded that the species combinations are largely determined by very special, local and often temporary conditions. A change in these conditions will largely alter the species composition of the coenosis. The species

richness in the Baltic area shows that it is possible for a relatively large number of aquatic macrophytes to grow together. A classification of different syntaxa is not given in this study because the very dynamic characteristics of the communities distinguished cannot be represented by the statis character of a phytosociological classification. This does not mean that such an approach has no use for general descriptions. At this moment, however, essential information is needed with respect to the life-strategies of the species and the processes which play a role in the co-existence of species. When this information has become available, it will be possible to make a better classification based on more, relevant data.

STRUCTURAL ASPECTS OF THE VEGETATION

In this section the structural aspects of the different communities with *Zannichellia* taxa will be discussed. Further, some processes involved in the genesis of several structural features are summarized. The structural aspects of brackish and freshwater habitats that will be considered are the floristic composition, the spatial organization in horizontal and vertical patterns, the growth-forms of the aquatic macrophytes and the relations between these components (den Hartog, 1978, 1979).

Horizontal and vertical patterns

Verhoeven (1980a) distinguished three types of horizontal pattern when discussing the brackish *Ruppia*-dominated phytocoenoses; facies, mosaic stands and purely mixed stands. Since the same aquatic macrophyte species can be found in all three categories, it is obvious that the patterns are not just the result of plant characteristics but that some dynamic processes must be involved. Before discussing these processes, some points are made with respect to the niche and habitat concept. Braakhekke (1980) summarizes several possible causes of the species richness of grassland phytocoenoses. In this study a survey is given of terms frequently used with respect to the processes involved in the co-existence of species. When using the term habitat, spatial relationships of the macrophyte to the environment are indicated, whereas the niche concept refers to the functional relationships of a macrophyte to its environment.

The horizontal patterns found in the phytocoenoses of this study concerning the *Zannichellia*-dominated ecosystems are caused by several factors. According to their cause the following patterns can be distinguished.

(1) Horizontal patterns caused by differences in the factors acting in a vertical direction. As examples, water-level fluctuations and the resulting desiccation, turbidity and light penetration, hydrostatic pressure and depth can be mentioned. These horizontal patterns can often be seen as zonations.

(2) Horizontal patterns caused by horizontal heterogeneity. Differences in sediment distribution and water circulation can give rise to mosaic patterns of different aquatic macrophytes.

(3) Horizontal patterns caused by functional differences within a rather uniform habitat. These differences are observed as mixed stands of (e.g.) *Z. pedunculata* and *Potamogeton pusillus.*

(4) Horizontal patterns caused by temporary environmental stress. Such patterns are often seen as facies.

Vertical patterns are not obvious in *Zannichellia*-dominated communities. The habitats are often very shallow with a gradually declining bottom. According to den Hartog (1978), the vertical patterns observed in aquatic macrophyte communities can be considered as consisting of zonation and stratification. Horizontal and vertical patterns are, however, functionally interlinked and therefore not easily separated with respect to their origin.

In a previous section some of the processes responsible for the separate distribution of aquatic macrophytes were discussed in relation to the chlorinity of the water. When cyclic phenomena are present at a fixed level and interval (chlorinity regime, removal of waterplants at the end of the growing season), no large changes will be observed in the following years with respect to the number of aquatic macrophyte species present in the brackish habitats. If, however, the cyclic phenomena alter, certain life-cycle stages of the aquatic macrophytes will suddenly have to cope with unusual environmental stresses and these species will risk local extinction. When comparing two situations in western Europe, viz. the littoral zone in a Baltic bay and a small, semi-isolated brackish ditch in The Netherlands, the following considerations are relevant. Under the prevailing chlorinity conditions in the Baltic, the environmental heterogeniety is considerable. Due to differences in water circulation, the depth of the water and currents, a variety of sediments can be observed. The result of this heterogeneity is a large number of (sub-)habitats. As summarized earlier a large number of aquatic macrophytes are present and form a vegetation with changing patterns of zonation and mosaics. When the environmental conditions in some localities change to such an extent that species become locally extinct, these particular species can often be found again nearby, often in the same habitat.

The dynamics of the habitat can lead to a gradual shifting of the plants in the direction of formerly unfavourable places. When this involves a species entering a population of some other aquatic macrophyte the former has to be able to inhabit a niche if co-existence is to be successful. The shifting of the middle points of *Zannichellia* populations could be observed in the Tvärminne area. When studying the quantitative aspects of the communities with *Zannichellia* taxa, a *Z. palustris* ssp. *repens* stand was observed for several months. This population appeared to develop in a fixed direction. Within two months, the population shifted over a distance of several metres. At one side of the population the plants died off and at the other side new horizontal runners were produced. This phenomenon was probably due to changing environmental conditions resulting in a development in one direction. However, the total number of aquatic macrophytes present in one place remained fairly constant.

These processes appear to have little effect in small brackish ditches in The Netherlands, where the environmental heterogeneity is much smaller. When environmental conditions become temporary unsuitable, the chance of becoming extinct in such a habitat is rather large because of the lack of refuge. The species that survive can even show mass development because of the lack of interference (negative interaction). The facies often observed in some brackish waters (Verhoeven, 1980a—*Ruppia* stands; den Hartog, 1963—*Potamogeton pectinatus* stands) are probably due to these effects.

Since in brackish water the distribution patterns of aquatic macrophytes (excluding the algae) are not so obviously determined by eutrophic or oligotrophic conditions as in fresh waters, the Cl^- factor can be regarded as being rather vital in these processes. Recolonization depends on the following factors.

(1) The dominant life-cycle stage present when the extinction factor was introduced (season-dependent). When seeds, tubers or turions are present which are resistant to the extinction factor, a rapid recolonization of plants can be expected.

(2) The number of diaspores produced (species-dependent).

(3) The number of different types of diaspores that can be produced (species and season-dependent).

(4) The viability of the various diaspores (species and season-dependent).

(5) Diaspores being transported from other habitats (by birds etc.) when there are no viable diaspores in the habitat under discussion.

It is obvious that the life-cycle and habitat characteristics play an important part in the disappearance and reappearance of aquatic macrophytes in a habitat. Since the number of species also influences the horizontal and vertical patterns in a vegetation, e.g. by competition, the characteristics must be also relevant to these patterns. The vegetation stands of small brackish habitats (e.g. ditches in The Netherlands) are often made up of very few species. When a species disappears its place is slowly filled up by the remaining species. Such a habitat, because of its small size and sheltered character, is often rather uniform with respect to sediment composition and wave action, and dominant environmental factors (such as the chlorinity) do not change in space but in time. Therefore, at a given moment in time the vegetation is rather uniform (sometimes monospecific) and is characterized as a facies.

In the larger area of the Baltic, however, the chlorinity factor is constant but factors such as wave action, depth and sediment constitution can differ within a small area. The various habitats of any species are separated in space. This means that several species occur at the same time in different places. Given favourable transport conditions, seeds, turions or plant fragments will quickly reach any empty spaces. Therefore the species are to be found in mosaics or mixed stands. From these considerations it follows that in a large habitat with an overall fluctuating chlorinity the vegetation pattern to be expected is one of facies or mosaic stands. In the large brackish étangs in southern France this has been frequently observed.

It is important to realize that the chlorinity of the water probably affects all plants in a rather simple way by increasing the osmotic pressure. There may be differences in the way different plants manage to survive this stress but in general this factor has a similar effect on plants

When discussing a factor such as the sediment composition it has to be realized that plants can take up different amounts of nutrients from these sediments. In a habitat with an apparently low environmental diversity regarding nutrient contents the different uptake by the various water plant species leads to niche differentiation.

In freshwater habitats there is no chlorinity stress In the littoral zone of a large lake, such as Lake Constance, a large environmental heterogeneity occurs as a result of temporary and local water-level fluctuations. Due to differences in the life-cycle (*Z palustris* ssp *repens* occurs in habitats where no water is left in the winter, *Potamogeton perfoliatus* occurs in deep, permanent water) and growth-form (*Utricularia* in sheltered places because of its Ceratophyllid character, *Nymphaea* in sheltered places because otherwise it would be damaged by the wind or currents) the observed patterns are primarily caused by habitat selection resulting in mosaic and mixed vegetation stands. When eutrophication occurs also it causes an overall alteration in the turbidity and detritus formation. Several species cannot survive this stress and disappear. There is no short-term replacement because none of the remaining species have the special abilities needed to inhabit these empty places. Therefore, barren areas are found here and there.

A totally different situation is encountered in a rather uniform habitat resulting from a uniform depth over a large area. In such environments there is no special advantage in certain life-cycle characteristics or growth-forms as described above. The overall effect of the eutrophication differs totally from the overall effect of (e.g.) a lethal chlorinity shock in brackish water. The changed sediment constitution and the changed nutrient content of the water offer the aquatic macrophytes a changed element ratio. Some macrophytes will grow better, other worse. Differences in growth are caused by different processes at the same place. In such situations mixed stands often occur.

In Fig. 13 frequently-encountered structural patterns of vegetation stands with *Zannichellia* taxa are schematized. In Fig 13A, the spatial organization of the littoral zone in a bay of the Gulf of Finland is indicated, illustrating the different distribution patterns with respect to depth and wave action of *Z. palustris* ssp. *repens* and *Z major* The zonation patterns are considered to be the result of the strong impact of the ice-cover in winter in the relatively shallow parts, resulting in plant specimens dying off and a favourable position for annual species The species composition and the spatial arrangement as found in the communities with *Z pedunculata*, *Potamogeton pectinatus* and *Ranunculus baudotii* in isolated pools, the margins of which dry out, was discussed by Van Vierssen and Verhoeven (1982) and is illustrated in Fig. 13B. In the temporary habitats in the Camargue (France) with stands of

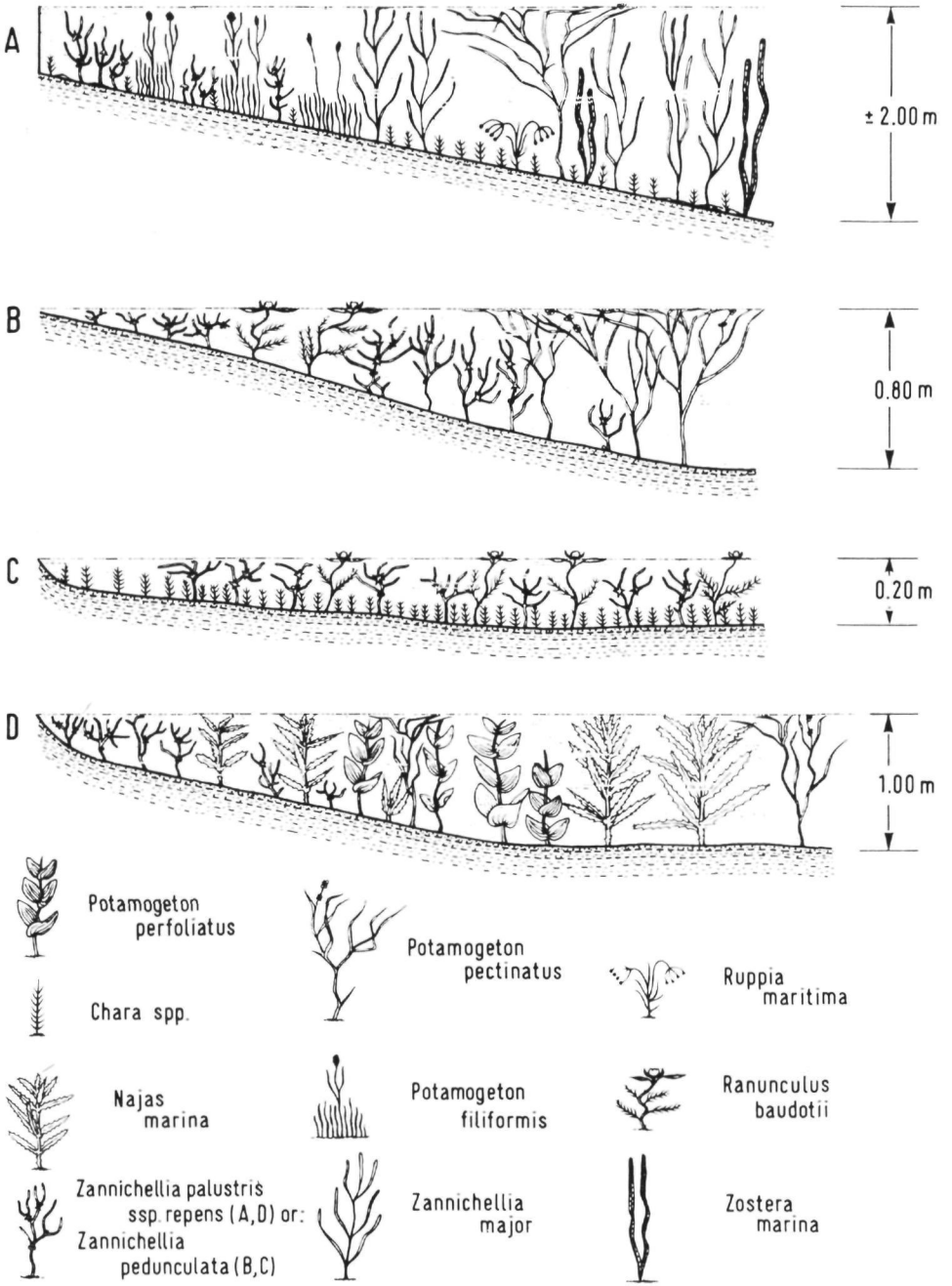


Fig. 13. Schematic representation of vegetation stands with *Zannichellia* taxa under field conditions. A, bay near Tvärminne, Finland. B, temporary pool, The Netherlands. C, temporary marsh, Camargue, France. D, former river bed, Lith, The Netherlands.

Z. pedunculata, there are no zonation patterns but mixed stands of aquatic macrophytes. In the Camargue the Characeae are of great importance and cover large areas (Fig. 13C). The freshwater habitats in the large lakes are usually characterized by clear zonations. Since the depth ranges are more limited in a habitat such as that in Lith (The Netherlands), the zonation patterns are less pronounced but still obvious. In Fig. 13D the spatial organization of this community is illustrated.

Growth-forms

Table X gives the number of different growth-forms in the coenoses of the three *Zannichellia* species. The growth-forms are categorized following Hutchinson (1975). This survey is presented because of the relationship between the different growth-forms and the fauna, which has caused similar growth-forms to be regarded as one category. Two figures are given in each

TABLE X

Comparison of growth-form range in coenoses with *Zannichellia* taxa

1			2	3	4			5	6	7	8	
Natopotamids	Hydrocharids	Nymphaeids	Magnopotamids	Parvopotamids	Myriophyllids	Ceratophyllids	Utriculariids	Lemnids	Ricciellids	Batrachiids	Charids	
												Zannichellia pedunculata
0			0	77	7			0	0	0	16	Baltic (7)
0			0	100	29			0	0	0	58	
2			1	55	7			20	8	6	1	The Netherlands (88)
6			3	100	23			68	34	24	3	
1			3	39	11			16	4	12	14	Camargue (60)
5			13	100	53			58	23	68	80	
												Zannichellia palustris
0			0	79	6			2	0	0	13	Baltic (12)
0			0	100	17			8	0	0	67	
7			26	52	7			4	0	0	4	Fresh waters (7)
14			57	100	29			14	0	0	14	
												Zannichellia major
0			0	86	3			0	0	0	11	Baltic (7)
0			0	100	14			0	0	0	57	

growth-form category; the upper represents the percentage of the total number of growth-forms found in the relevés, the lower indicates the frequency of occurrence of each growth-form in the relevés. As can be seen from this table, the communities with *Z. pedunculata* in the Baltic are mainly characterized by the parvopotamid and, to a lesser extent, the charid growth-form. It is obvious that the character of the coenoses changes with the latitude. In the Camargue, the parvopotamid growth-form is less important than the batrachiid growth-form. The charids are of great importance in this area, in contrast to The Netherlands where this group of algae has almost completely disappeared because of the heavy eutrophication. The phytocoenoses in the Baltic area with *Z. palustris* ssp. *repens* and *Z. major* are characterized by the same growth-forms as those with *Z. pedunculata* In the fresh waters of southern latitudes other groups, such as the magnopotamids, the natopotamids*, hydrocharids and nymphaeids besides the group with the myriophyllids, ceratophyllids and utricularids, characterize the phytocoenoses with *Z. palustris*

Seasonal aspects

In phytocoenoses with *Zannichellia* taxa different seasonal aspects can be distinguished, e.g., species which develop at the end of the season will be found in permanent waters but not in habitats that are dry then. The early germination of seeds, and even the early seed production by plants of *Z. pedunculata*, means that the areas which dry out earliest often become inhabited by *Z. pedunculata* after refilling. Species such as *Ruppia maritima* var. *maritima* and *Potamogeton pectinatus* reach their optimum later in the season. This is partly due to a difference in timing of seed germination and tuber-budding and partly to obvious differences in the rates of plant development. The seedsetting of *Ruppia maritima* var. *maritima* is later than that of *Z. pedunculata.* In a brackish polder water in Zeeuws-Vlaanderen (The Netherlands), the first *Z. pedunculata* seeds were recorded on June 8th, whereas under the same conditions *Ruppia maritima* var. *maritima* seeds appeared for the first time on August 3rd. *Potamogeton pectinatus* developed out of tubers in relatively deep polder water. The different maximum biomasses of these macrophytes were recorded at different times in the growing season. *Z. pedunculata* reaches its optimum early in summer, *Ruppia maritima* var. *maritima* is dominant in summer and *Potamogeton pectinatus* has its optimum in late summer and autumn.

Similar seasonal aspects were observed in stands with *Z. palustris* ssp. *repens.* In spring and early summer (May, June) this taxon fructified abundantly in the very shallow border zone of the sampling station of Lith (The Netherlands). As the water-level went down these habitats dried out and the plants

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*The natopotamids are given separately from the nymphaeids because they are considered to differ essentially from them.

died, leaving numerous seeds in the sediments. The development of *Najas marina*, the dominant macrophyte, in August was much slower. This annual species develops out of seeds which germinated some weeks later (up to more than a month) than those of *Z. palustris* ssp. *repens*. As was described by Van Vierssen (1982b), the germination of *Najas marina* seeds (collected in October in the same water) was very good after stratification of several months (4°C). The seeds germinated well under conditions of low oxygen tension and a relatively high optimum temperature (24°C). Daylight conditions inhibited germination up to 20°C, even when the oxygen tension was low. The relatively late development of *Najas marina* during the growing season, as indicated by Luther (1951b) and as observed in Lith, is probably caused by the germination ecology. In the relatively shallow littoral zone at the beginning of the summer the light conditions are too bright and the temperatures too low for its germination. Only later in the summer is sufficient shade provided by other macrophytes and are the temperatures high enough for good germination.

As the discussed *Zannichellia* taxa develop early in the growing season their abundance in the habitats is totally changed when these are revisited some weeks or months later. This applies specially to freshwater ditches near brackish habitats. In spring *Z pedunculata* only was observed but, after a time, freshwater species such as *Elodea nuttallii* (Planch.) St. John, *Ceratophyllum demersum*, *Myriophyllum spicatum* and *Potamogeton natans* L. were abundant.

Discussions and conclusions

From the previous sections it follows that a great number of different processes determine the vegetation patterns in the field. Species have been observed to occur in different vegetation patterns that are considered to be the result of habitat or niche differentiation or both. Some species appeared to be able to take advantage of different special abilities under different environmental conditions. An important distinction has to be made between occurrence because of special life-cycle characteristics (e.g , drought-resistant seeds) and occurrence because of special physiological characteristics of mature plants (e g., specialized uptake of certain nutrients). Because the environmental conditions which lead to spatial differentiation (habitat differentiation) often occur over relatively wide areas, the resulting patterns are different from those caused by functional differentiation (niche differentiation) between plants, which can occur within a very limited area (e.g., several mm^2). It is, however, also possible that within a limited area habitat differentiation occurs (e.g., roots at different depths). Within one community habitat and niche differentiation seem related to the vegetation patterns to a certain extent. In general, the habitat differentiation in communities with *Z. pedunculata* results in rather coarse patterns. These patterns can be recognized in space and also in time. In the brackish ditches with a seasonal separation of the maximum biomass of *Z. pedunculata* and *Potamogeton pectinatus*

the habitat differentiation takes place in time This separation is considered as habitat differentiation too, because at the time *Potamogeton pectinatus* reaches its maximum biomass the chlorinity has reached such high levels that *Z pedunculata* slowly dies In fact two different habitats occur in time

As Van Vierssen (1982c) postulates, it is also very likely that a certain degree of niche differentiation occurs between *Z pedunculata*, *Potamogeton pectinatus* and *P pusillus* and *Ruppia* species by means of a selective uptake of elements Such a differentiation enables species to occupy the same habitat without excluding each other. The vegetation patterns are less coarse as a consequence

In fact too little information is available to explain all the patterns observed. It is only in a few cases that the causes of the observed patterns become obvious The zonation in *Z pedunculata* dominated communities can be relatively easily understood (drought-resistant seeds) but the life-strategies of a very large number of aquatic macrophytes are still completely unknown The study of the germination of seeds, tubers and turions may be relatively simple, but the study of the competition for essential elements between plants is much more complicated It is obvious that much more autecological and synecological data are needed to understand the underlying processes of vegetation patterns as observed in the field

MICROCLIMATIC CONDITIONS

The communities and their horizontal and vertical organization are of great importance for the aquatic macrofauna inhabiting the phytal zone The impact of a factor such as the drying out of a habitat on the faunistic species composition may be obvious, but less obvious environmental factors, such as the diurnal oxygen fluctuations or the carbonate content, temperature, ammonia concentrations and the pH, may also be relevant In this section a general survey will be given of the most relevant factors in three different types of vegetation, respectively dominated by (1) parvopotamids, viz *Potamogeton pectinatus*, *P pusillus* and *Z pedunculata* (community as described under A7, see p 85), (2) a natopotamid, viz *Potamogeton natans*, and (3) a mixture of a myriophyllid, *Myriophyllum spicatum* and parvopotamids, viz. *Z pedunculata*, *Potamogeton pectinatus* and *P pusillus* The environmental factors studied are the temperature of the water and the air, the diurnal fluctuations of the carbonate—bicarbonate system together with the pH fluctuations, as influenced by the different macrophytes In the phytocoenoses with *Potamogeton natans* L , the influence of the floating leaves of this natopotamid is studied by comparing areas with and without floating leaves.

Material and methods

The study of the diurnal variation was carried out on the island of Terschelling (The Netherlands). Three sampling stations were chosen with com-

munities containing different types of aquatic macrophytes. The pH and the temperature were assessed under field conditions. Water samples were collected in ethylene bottles and analysed within 15 min after collection. The oxygen concentrations were assessed by means of titrations according to Winkler, the CO_2, HCO_3^- and CO_3^{--} concentrations were assessed by means of a titration with NaOH and HCl solutions in relation to pH changes. The assessments of the different concentrations were carried out in duplo. The means are given in the results.

The insolation was quantified with a Licor quantum photometer. The water temperature was measured 15 cm underneath the water surface, and the air temperature was measured 10 cm above the water surface. To get an impression of the oxygen produced by the seston some experiments with light and dark bottles were carried out during a period of several hours to assess the share and importance of this production in comparison with the oxygen production of the community. The bottles were placed halfway between the bottom and the water surface.

Results

The results of these studies are summarized in three figures. In Fig. 14, the results for the phytocoenoses with *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* are illustrated. It is obvious that the air temperature is subject to quicker fluctuations than the temperature of the water. However, because of the rather small size of the habitat (a small ditch, see Fig. 6D) the time lag between the rise of the air temperature as a result of daily fluctuations and the rise of the temperature of the water is rather short. The effect of the plant mass on the diurnal oxygen fluctuations is considerable. During the period between 06.30 and 12.00 h, the net oxygen production by the seston was assessed. This production resulted in a net increase of 0.245 mg O_2 per l. The production of the macrophyte—epiphyte complex is alone responsible for more than 98% of the net oxygen production. A significant oversaturation between approximately midday and 21.00 h and a very low oxygen concentration during the early hours of the following day were observed. The diurnal carbonate—bicarbonate concentrations fluctuated as a result of the CO_2 consumption of the waterplants and the consequent changes of the chemical equilibria. The pH increased rapidly up to midday and stayed at the same level until the evening.

The total insolation was significantly smaller in the community with *Myriophyllum spicatum*, *Potamogeton pectinatus* and *P. pusillus*. The net oxygen production of the plant—epiphyte complex, however, caused very high levels of oxygen in this ditch environment. No large differences were observed when compared with the *Zannichellia*-dominated system. The same general tendency to consume the CO_2 present, with a resulting increase of the pH, was observed (Fig. 15). The concentrations which were found were of the same order of magnitude.

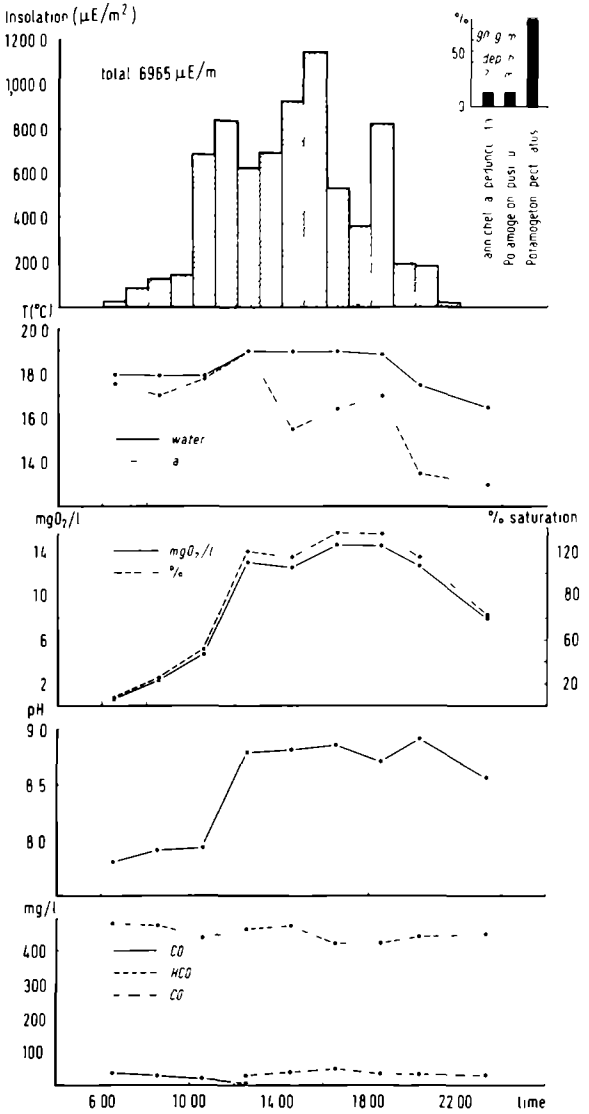

Fig. 14. The course of a number of abiotic parameters in a ditch on Terschelling (sampling station 2, during one day (August, 1979) in a community with *Zannichellia pedunculata*, *Potamogeton pectinatus* and *Potamogeton pusillus* The inset shows the share of these macrophytes in the total biomass. The biomass figure in the inset gives the total ash-free dry weight of the macrophytes.

The third system studied, a small ditch with dominant stands of *Potamogeton natans*, exhibits clear differences when compared with the other two communities. The differences between the samples taken underneath the floating leaves of *Potamogeton natans* and those taken between

Potamogeton pusillus specimens (in Fig. 16 indicated as 'open water' because of the absence of floating leaves) are obvious. The differences in oxygen concentration between these two micro-habitats are striking. The mean level of the concentration is significantly lower than in the coenoses discussed above. During the entire sampling period CO_2 was present, as was HCO_3^-.

The pH reached levels not exceeding 8.0.

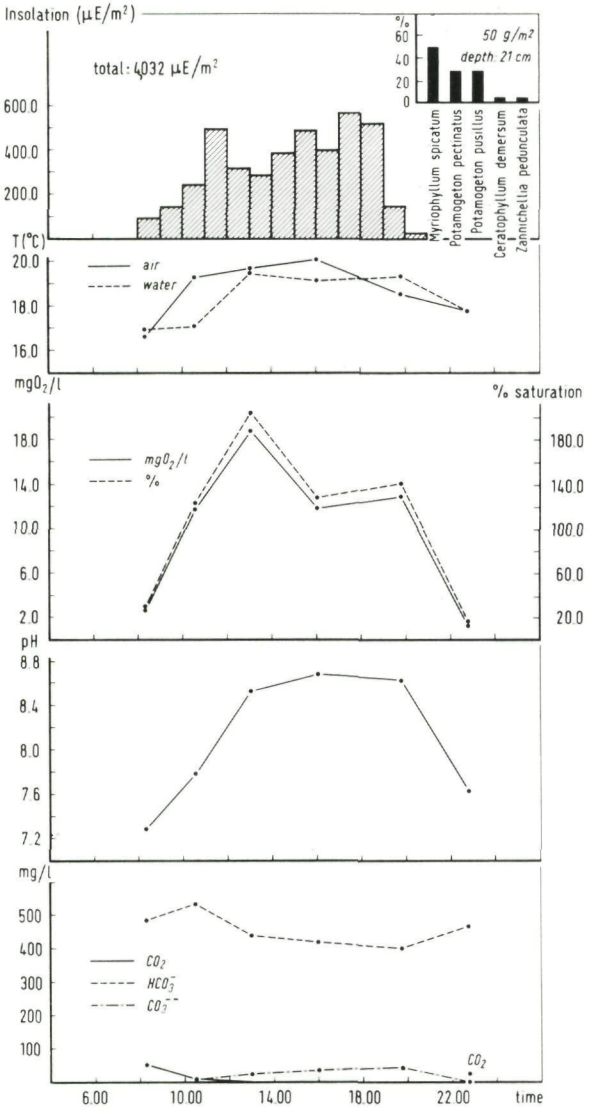

Fig. 15. The course of a number of abiotic parameters in a ditch on Terschelling (sampling station 6, during one day (August, 1979) in a community with *Myriophyllum spicatum*, *Potamogeton pectinatus*, *Potamogeton pusillus*, *Ceratophyllum demersum* and *Zannichellia pedunculata*. The inset shows the share of these macrophytes in the total biomass. The biomass figure in the inset gives the total ash-free dry weight of the macrophytes.

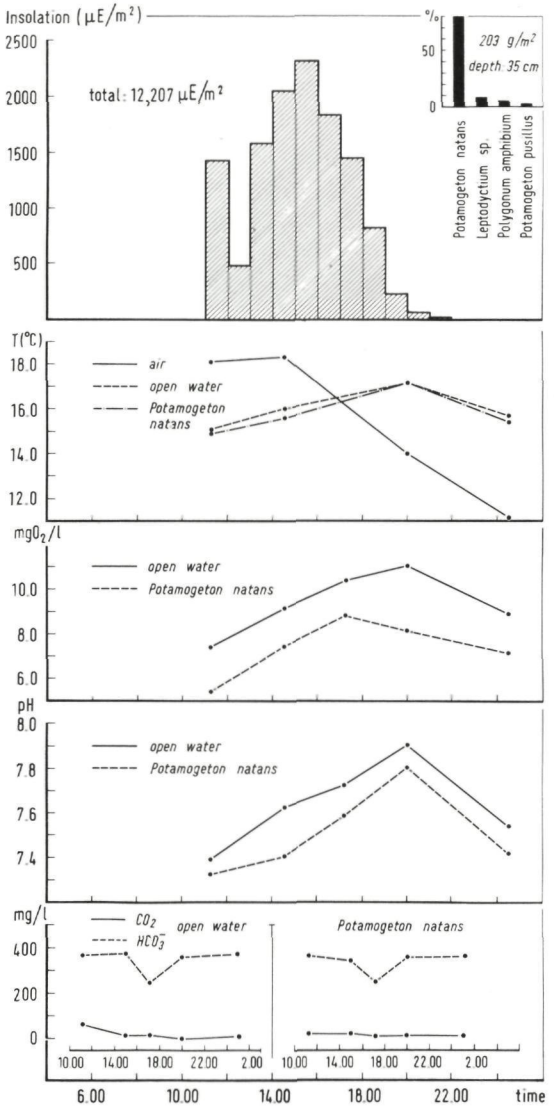

Fig. 16. The course of a number of abiotic parameters in a ditch on Terschelling (sampling station 8, during one day (August, 1979) in a community with dominant stands of *Potamogeton natans*. The inset shows the share of this macrophyte in the total biomass. The biomass figure in the inset gives the total ash-free dry weight of the macrophytes.

Discussion and conclusions

It is obvious that the diurnal fluctuations of the oxygen concentrations are considerable. Due to the relatively small size of the habitat and the relatively large biomass, the oxygen levels are subject to large fluctuations. As Sculthorpe (1967) indicates, it is not only the oxygen levels but also the CO_2 levels, the pH and the ammonia concentrations which are of immediate importance to the fauna inhabiting these phytocoenoses. The CO_2

levels, however, are very low and this gas is often not detectable. According to this author the rising pH could be damaging, but only at pH levels exceeding 10 Further, it is obvious that the floating leaves cause differences in temperature within the vegetation, but this environmental heterogeneity is also present in the parvopotamid system, although less pronounced. More elaborate studies of temperature conditions as influenced by growth-form characteristics of aquatic macrophytes were carried out by Dale and Gillespie (1976, 1977a & b, 1978) and Morris and Barker (1977).

SPECIES COMPOSITION OF FAUNA IN RELATION TO MACROPHYTES AND ENVIRONMENTAL CONDITIONS

Introduction

The aim of this section is to discuss the species composition of the fauna of the brackish phytocoenoses described on pp. 80—97 and to establish the relation between these species and the structural aspects of the phytocoenoses. This discussion will be restricted to the brackish communities classified in the category A of *Zannichellia* taxa communities (p 80) This restriction has been made because it was only from these types of ecosystems that sufficient data were collected to be able to compare different geographical areas in western Europe Within the scope of this study the fauna will be briefly discussed More detailed information will be published elsewhere. The quantitative aspects of the fauna and vegetation will be discussed below (p 134)

Material and methods

The macroscopic fauna (> 1 mm) has been collected in three major areas; Finland (Tvarminne area), The Netherlands and France (Camargue) The brackish-water fauna in the Tvarminne area was sampled in the summer of 1980 in a vegetation with *Z major* (A2) and in one with *Z palustris* ssp. *repens* (community type A1) During the same summer, three localities in the Camargue (France) were studied (ditch near Salin de Giraud, community type A11, a ditch near Salin de Badon, community type A10—A11, marsh at Le Paradis, community type A11) In The Netherlands sampling was more frequent. The aquatic and semi-aquatic fauna was sampled with a dip-net (mesh-width of 0.5 mm). Samples of the substrate were also collected and sieved to obtain the benthic (in-) fauna.

Results

The results will be discussed separately for the different areas studied.

Gulf of Finland (Tvarminne, Finland)
Table XI gives a list of the species which were collected in the phytoco-

TABLE XI

Distribution of fauna in Tvärminne (Finland)

Community type	A1	A2		A1	A2
Planaria torva (Muller)	+	+	*Bathyporeia pilosa* Lindstr		+
Electra crustulenta (Pallas)	+	+	*Corophium volutator* (Pallas)		+
Oligochaeta	+	+	*Macroplea mutica* F		+
Nereis diversicolor (O F Mull)	+	+	*Mya arenaria* L		+
Neomysis vulgaris (Thompson)	+	+	*Halocladius variabilis* (Staeger)		+
Idotea chelipes (Pallas)	+	+	*Paratanytarsus* sp		+
Gammarus salinus (Spooner)	+	+	*Manayunkia aestuarina* (Bourne)	+	+
Macoma baltica (L)	+	+			
Mytilus edulis L	+	+	*Asellus aquaticus* L	+	
Cerastoderma glaucum (Poiret)	+	+	*Palaemon squilla* (L)	+	
Hydrobia ulvae (Pennant)	+	+	*Potamonectus depressus* (Fabr)	+	
Hydrobia ventrosa (Montagu)	+	+	*Piona pusilla* (Neuman)	+	
Potamopyrgus jenkinsi (Smith)	+	+	*Pomatoschistus minutus* (Pallas)	+	
Theodoxus fluviatilis (L)	+	+	*Pungitius pungitius* (L)	+	
Cryptochironomus sp	+	+	*Lymnaea peregra* (Muller)	+	
Cladotanytarsus sp	+	+	*Lymnaea stagnalis* (L)	+	
Dicrotendipes gr *tritomus*	+	+	*Lymnaea palustris* (Muller)	+	
Dendrocoelum lacteum (Muller)		+	*Sigara striata* (Fieb)	+	
Pygospio elegans Claparede		+	*Polypedilum* gr *bicrenatum*	+	
Piscicola geometra (L)		+	*Cricotopus* gr *sylvestris*	+	
Pontoporeia affinis Lindstr		+	*Chironomus* gr *halophilus*	+	
Pontoporeia femorata Kroyer		+	*Camptochironomus* sp	+	
Mesidotea entemon (L)		+	*Procladius* sp	+	
Idotea baltica L		+	*Ablabesmya* sp	+	
Jaera albifrons Leach		+	*Chironomus* gr *annularius/plumosus*	+	
Gammarus oceanicus Segerstråle		+			
Gammarus zaddachi Sexton		+			

enoses with *Z palustris* ssp. *repens* and *Z major*. The differences which were observed are mainly the result of differences in wave action, substrate and water turbulence since there are no large differences in the chlorinity of the water. As can be seen from Table XII Crustacea and Mollusca are important groups in the stands with *Z major* (A2). Relatively few Insecta occur in these communities. In the sampling station with *Z palustris* ssp. *repens* (A1), however, somewhat more freshwater species are present than in the communities with *Z. major* The communities consist of a mixed group of euryhaline marine species, true brackish-water species and euryhaline freshwater species with a dominance of the latter.

The Netherlands

As was stated before some taxonomical groups will be discussed separately. A classification made on the basis of the total fauna composition will be presented after this discussion.

TABLE XII

Community parameters of brackish-water coenoses

Area	Community type	Author	Species number	Composition I	M	C	P	Permanent + Temporary —	Composition F	B	M	H
Finland	A1—A2	This study	34—35	17	23	35	6	+++—	54	23	23	0
	C3—C4—C5 *Ruppia maritima*	Verhoeven, 1980a	13—24	8	29	29	4	+++—	13	35	52	0
	D3—D4 *Ruppia cirrhosa*	Verhoeven, 1980a	18—27	12	42	42	4	+++	20	32	44	4
The Netherlands	A6	This study	35	42	11	17	2	++—	43	31	23	3
	A7—A8	This study	14—70	59	12	9	0	+—	96	2	1	1
	A9	This study	2—30	76	7	3	0	—	97	3	0	0
	D1—D2—D3 *Ruppia cirrhosa*	Verhoeven, 1980a	9—34	44	6	17	9	+	32	44	12	12
	C2 *Ruppia maritima*	Verhoeven, 1980a	12—22	18	9	3	14	++—	14	59	18	9
France	A10—A11	This study	21—24	83	8	4		——	88	12	0	0
	B1—B2—B3—B4 *Ruppia cirrhosa*	Verhoeven, 1980a	5—21 (17)	6	20	23	6	++	0	65	29	6
	A2—A3 *Ruppia maritima*	Verhoeven, 1980a	10—13	46	7	15		——	25	75	0	0

I = Insecta, M = Mollusca, C = Crustacea, P = Polychaeta, F = Freshwater species, B = Brackish-water species, M = Marine species, H = Holeuryhaline species.
The number of + or — symbols indicate the relative importance of both characteristics.
The underlined figures are the maxima.

Coleoptera aquatica and semi-aquatica The distribution of the aquatic and semi-aquatic Coleoptera in the different sampling stations is summarized in Table XIII. A number of species occur in all community types. *Hygrotus inequalis*, *Laccophilus minutus* and *Helophorus brevipalpus* occur in more than 50% of all sampling stations. Among the frequently occurring species (present in 25%—50% of the sampling stations), a relatively large number are only present in semi-isolated, permanent habitats (*Laccobius minutus*, *Noterus clavicornis* and *Laccobius biguttatus*) Other species such as *Coelambus confluens* only occur in isolated and temporary habitats There are also numerous scarce species which occur only in the semi-isolated, permanent habitats. As Van Vierssen and Verhoeven (1982) pointed out, there exists a positive correlation between the number of species found in pools of the A9 community type and the total coverage of the aquatic macrophytes in these pools.

The chlorinity tolerance of the species is also an important factor *Helophorus aquaticus* and *Helophorus brevipalpus* are very salt-tolerant, ±18.5 and 11‰ Cl^- respectively. The maximum chlorinities tolerated by the numerous other species did not exceed ±6‰ Cl^-

Whether a species occurs or not in an isolated habitat is also determined by its capacity to reach such a habitat. The most frequently occurring species, *Helophorus aquaticus* and *Helophorus brevipalpus*, are very successful flyers (Landin, 1976; Landin and Stark, 1973). *Laccophilus minutus* and *Coelambus confluens* are good flyers too (Jackson, 1952, 1973) *Hygrotus inequalis* has a variable flight muscle development (Jackson, 1952, 1973) and is mainly restricted to the permanent semi-isolated ditches in the present study *Noterus clavicornis* lacks well-developed wings (Jackson, 1973) and is restricted to the permanent habitats

It has to be realized that the frequency in which certain species are found not only reflects whether the habitats are suitable or not but also gives information with respect to the population dynamics of a species. When the capacities to disperse are the same for two species, a species which usually occurs in relatively low numbers will be found less frequently in isolated habitats than a species that occurs in great numbers.

Diptera Table XIV gives a list of the Chironomidae larvae found in the sampling stations. They do not form a homogeneous group. The occasional Brachycera larvae usually belong to the genera *Ephydra* and *Hydrellia* the pupae of which are found on the leaves of Potamogetonaceae. The number of brackish-water Chironomidae is low. *Chironomus halophilus*, *Chironomus salinarius* and *Halocladius varians* indicate brackish water. They only occurred in the brackish A6 community in the present study. The other frequently occurring species are more or less freshwater species.

Heteroptera aquatica and semi-aquatica Table XV gives the distribution of the aquatic and semi-aquatic Heteroptera species In the brackish A6 communities only a few species occur because of the rather high chlorinities. The

TABLE XIII

Distribution of aquatic and semi-aquatic Coleoptera in The Netherlands

Table/ No. relevé	V 1	VI 4	VI 5	VI 6	VI 7	VI 15	VI 2	V 4	V 5	V 5	IV 33
Classification:	A6	A7	A7	A7	A7	A7	A7	A7	A7	A7	A8
Hygrotus inequalis (Fabr.)		+	+	+	+	+	+	+	+	+	+
Laccophilus minutus (L.)				+		+	+		+	+	
Helophorus aquaticus L.	+						+	+	+	+	+
Helophorus brevipalpis Bed.							+	+	+	+	+
Hydrobius fuscipes L.	+				+	+					
Haliplus apicalis Thoms.				+	+	+	+		+	+	
Hydroporus planus (Fabr.)						+		+			
Hydroporus palustris L.			+	+				+			+
Laccobius minutus (L.)		+			+	+		+	+	+	
Noterus clavicornis (Deg.)			+		+		+	+	+	+	+
Haliplus lineatocollis Marsh.	+	+		+		+				+	
Enochrus bicolor Fabr.							+				
Haliplus ruficollis Deg.				+			+		+	+	
Coelambus impressopunctatus (Schall.)								+			
Laccobius biguttatus Gerh.					+		+	+	+	+	
Coelambus confluens (Fabr.)											
Haliplus immaculatus Gerh.		+		+		+		+			
Enochrus testaceus Fabr.						+		+		+	
Noterus crassicornis (Müll.)								+	+	+	
Anacaena limbata Fabr.							+	+		+	
Spercheus emarginatus (Schaller)								+	+	+	
Haliplus fluviatilis Aubé			+			+					+
Agabus nebulosis Först					+						
Agabus bipustulatus (L.)								+			+
Agabus guttatus (Payk.)								+			+
Rhantus frontalis (Marsham)	+							+			
Laccobius bipunctatis (Fabr.)							+	+			
Colymbetes fuscus (L.)											
Gyrinus caspius Menetr.	+										
Peltodytes caesus (Duftschmidt)									+		
Agabus sturmi (Gyllenhal)							+				
Dytiscus circumflexus Fabr.								+			
Cercyon tristis Illiger							+				
Coelostoma orbiculare Fabr.								+			
Ochtebius dilatatus Stephens	+						+				
Ochtebius minimus (Fabr.)							+				
Hydrovatus cuspidatus (Kunze)										+	
Graptodytes pictus (Fabr.)										+	
Helochares lividus Forst.										+	
Laccophilus hyalinus (Deg.)		+									
Haliplus obliguus Fabr.											
Hygrotus decoratus (Gyll.)			+								
Anacaena globulus (Paykull)											+
Rhantus notatus (Fabr.)											
Ilybius fenestratus (Fabr.)											
Hydroporus erythrocephalus (L.)											+
	Permanent ←										

(1) Isolated pool in Zeeuws-Vlaanderen with monospecific vegetation of *Z. pedunculata*, not represented in relevés.

(2) For relevés see publication of van Vierssen and Verhoeven (1982).

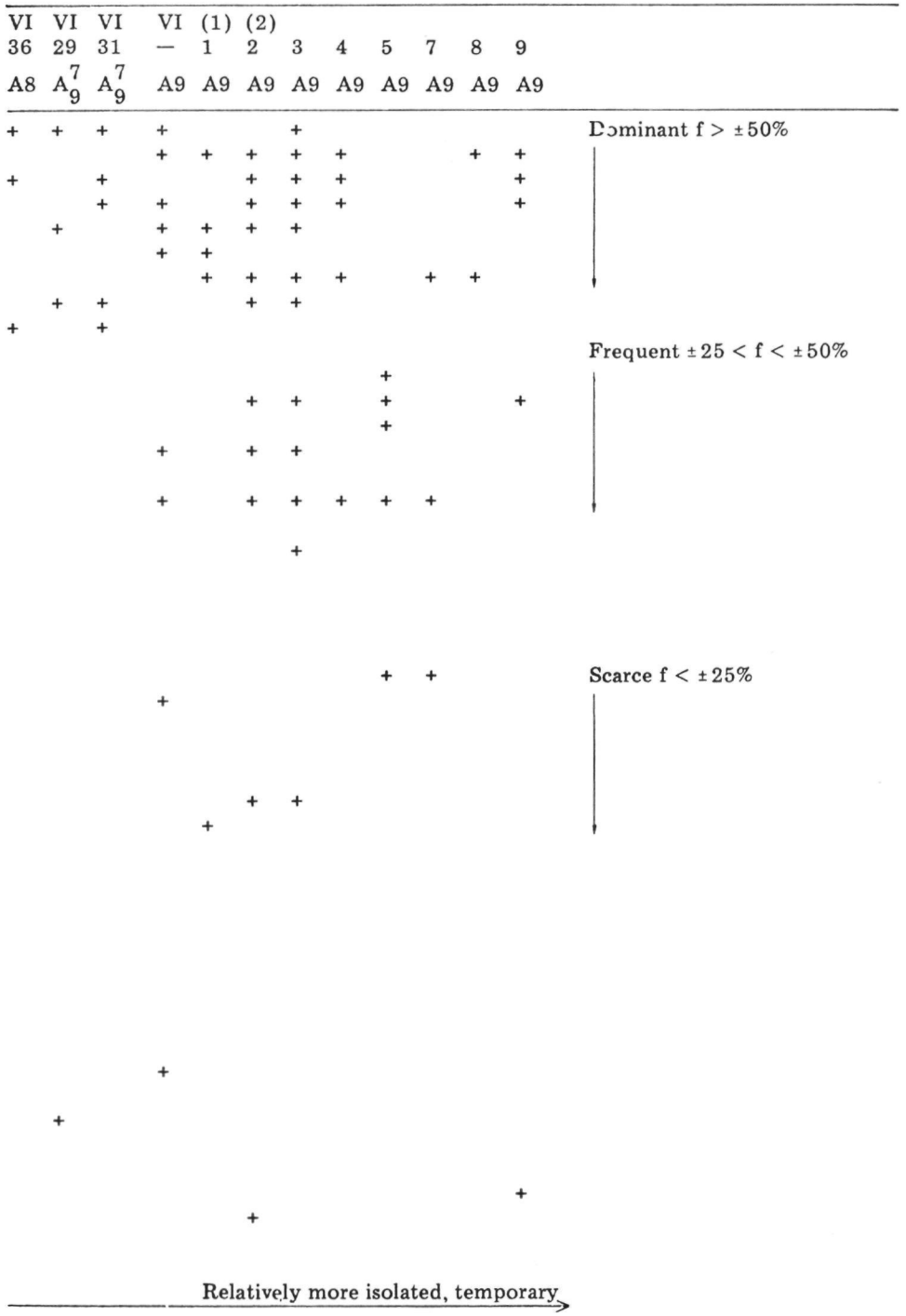
VI 36 A8
VI 29 A7 9
VI 31 A7 9
VI — A9
(1) 1 A9
(2) 2 A9
3 A9
4 A9
5 A9
7 A9
8 A9
9 A9
Dominant f > ±50%
Frequent ±25 < f < ±50%
Scarce f < ±25%
Relatively more isolated, temporary

TABLE XIV

Distribution of Chironomidae larvae in The Netherlands

Table/no. relevé	V 1	VI 4	VI 5	VI 6	VI 7	VI 15	V 2	V 4	V 5	IV 5	VI 31
Community type:	A6	A7	A7	A7	A7	A7	A7	A7	A7	A7	A7-A9
Cricotopus ornatus (Meigen)	+				+	+	+	+	+		
Chironomus spec.							+	+	+	+	
Glyptotendipes spec.							+	+	+	+	
Chironomus gr. *annularius/ plumosus*			+		+						+ +
Glyptotendipes barbipes (Staeger)			+		+						
Procladius s.a.							+	+		+	
Psectrocladius gr. *psilopterus*							+	+	+		
Polypedilum sp.							+	+	+		
Cryptochironomus sp.							+			+	
Acricotopus lucens (Zetterstedt)								+	+		
Chironomus piger Str.											+
Parachironomus varus Goetghebuer						+					
Parachironomus mauricii Krus.		+									
Procladius choreus (Meigen)						+					
Tanypus kraatzi (K.)										+	
Cricotopus gr. *sylvestris*										+	
Endochironomus gr. *signaticornis*										+	
Endochironomus gr. *nymphoides*										+	
Parachironomus gr. *arcuatus*										+	
Microchironomus tener (Kieffer)										+	
Pentapedilum sp.										+	
Palpomyia sp.										+	
Xenopelopia sp.								+			
Psectrocladius gr. *barbimanus*									+		
Corynoneura sp.									+		
Halocladius varians (Staeger)	+										
Chironomus salinarius Kieffer	+										
Chironomus halophilus Kieffer	+										

absence of a number of species in the isolated and temporary A9 communities is caused by the high chlorinities as well as by the isolated character of these habitats. The most frequently occurring species are *Sigara lateralis*, *Sigara striata*, *Sigara stagnalis*, *Corixa punctata* and *Corixa affinis*. Some general distribution patterns of these species in relation to the chlorinity of the water and the vegetation coverage in brackish waters in The Netherlands have been discussed by Van Vierssen and Verhoeven (1982). *Sigara lateralis* and *Sigara stagnalis* are the only two corixids at relatively high chlorinities (±6‰) and in sparse vegetation stands. *Corixa punctata*, *Corixa affinis* and *Sigara striata* join these two species at lower chlorinities (±4‰) and when the vegetation coverage is higher than about 60%.

Mollusca. Table XVI gives the species composition in the sampling stations.

TABLE XV

Distribution of aquatic and semi-aquatic Heteroptera in The Netherlands

Table/no. relevé:	V 1	VI 4	VI 5	VI 6	VI 7	VI 15	V 2	V 4	V 5	IV 5	VI 33	VI 36	VI 31	(1) x	(2) 1	2	3	4	5	7	8	9	11	12
Classification:	A6	A7	A7	A7	A7	A7	A7	A7	A7	A7	A8	A8	A7 A9	A9	A9	A9	A9	A9	A9	A9	A9	A9	A9	A9
Sigara lateralis (Leach)	+				+	+	+	+	+	+			+	+	+	+	+	+	+	+		+	+	+
Sigara striata (Fieb.)		+	+	+	+	+	+	+	+	+		+	+		+	+	+		+		+	+	+	
Corixa punctata (Illiger)	+	+		+			+	+	+	+				+	+	+	+	+	+	+	+	+	+	
Sigara stagnalis (Leach)	+	+			+		+	+	+					+	+	+	+	+	+	+		+	+	+
Corixa affinis Leach		+					+	+	+					+	+	+	+	+	+	+	+	+	+	
Gerris thoracicus Schumm.		+		+			+		+	+					+	+	+		+				+	
Hesperocorixa linnei (Fieb.)		+	+	+					+	+	+					+	+			+			+	
Callicorixa concinna (Fieb.)							+		+	+				+			+	+		+		+		
Sigara falleni (Fieb.)		+		+				+		+						+					+			
Notonecta glauca L.		+								+						+	+		+	+				
Callicorixa praeusta (Fieb.)							+	+	+								+							
Nepa rubra L.			+			+			+			+												
Hesperocorixa sahlbergi (Fieb.)				+				+			+													
Plea leachi Mcgreg. & Kirk							+			+				+										
Corixa panzeri (Fieb.)		+												+										
Hydrometra stagnorum (L.)								+	+															
Notonecta viridis Delc.										+				+										
Gerris lacustris (L.)								+																
Ilyocoris cimicoides (L.)									+															
Cymatia coleoptrata (Fabr.)									+															

(1) Isolated pool in Zeeuws-Vlaanderen with monospecific vegetation of *Zannichellia pedunculata*, not represented in relevés.
(2) For relevés see van Vierssen and Verhoeven (1982).

TABLE XVI

Distribution of Mollusca in The Netherlands

Table/no. relevé:	V 1	VI 4	VI 5	VI 6	VI 7	VI 15	V 2	V 4	V 5	IV 5	VI 33	VI 36	VI 29	VI 31
Classification:	A6	A7	A7	A7	A7	A7	A7	A7	A7	A7	A8	A8	A^{7}_{9}	A^{7}_{9}
Hydrobia ulvae (Pennant)	+													
Hydrobia ventrosa (Montagu)	+													
Cerastoderma glaucum (Poiret)	+													
Lymnaea peregra (Müller)		+	+	+	+	+	+	+	+	+	+	+	+	+
Planorbis planorbis (L.)		+	+	+		+	+	+	+	+	+	+		
Lymnaea palustris (Müller)		+	+	+		+	+	+	+					
Potamopyrgus jenkinsi (Smith)	+		+		+		+	+	+		+	+		+
Bithynia tentaculata (L.)		+	+	+				+		+				
Physa fontinalis (L.)		+		+			+			+			+	
Gyraulus albus Müller			+				+	+		+			+	
Armiger crista (L.)			+				+	+	+	+				
Planorbis corneus (L.)		+		+						+		+		
Lymnaea stagnalis (L.)		+		+						+				
Bithynia leachi (Sheppard)								+	+					
Anisus vortex (L.)							+		+					
Bathyomphalus contortus (L.)											+			
Segmentina complanata (L.)										+				
Anodonta anatina (L.)										+				
Valvata piscinalis (Müller)										+				

In the A6 community type, two brackish-water and one marine species occur; *Hydrobia ventrosa*, *Cerastoderma glauca* and *Hydrobia ulvae* respectively. The most frequently occurring species in the other community types are *Lymnaea peregra*, *Lymnaea palustris*, *Planorbis planorbis* and *Potamopyrgus jenkinsi*. The absence of Mollusca in the temporary pools (A9 community type) is striking. The reasons for this absence are the isolation of these pools, the strongly fluctuating chlorinity and the fact that they occasionally dry out.

Hydrachnellae. The species composition in the sampling stations is given in Table XVII. In the brackish A9 communities a very low number of species occurs. Only *Hydrachna conjecta*, *Hydrachna cruenta*, *Piona alpicola* and *Limnesia undulata* are found frequently.

TABLE XVII

Distribution of Hydrachnellae in The Netherlands

Table/No. relevé:	VI 4	VI 5	VI 6	VI 15	V 2	V 4	V 5	IV 5	(1) 2	4	7	8
Community type:	A7	A7	A7	A7	A7	A7	A7	A7	A9	A9	A9	A9
Hydrachna conjecta Koenike	+	+			+	+	+	+			+	+
Piona alpicola (Neuman)	+	+	+		+	+	+					
Limnesia undulata (Müller)	+	+	+	+			+					
Hydrachna cruenta Müller	+		+				+		+	+		
Hydrachna skorikowi Piersig					+	+						
Piona pusilla (Neuman)						+	+					
Arrenurus globator (Müller)							+					
Eylais extendens (Müller)						+						
Eylais hamata Koenike					+			+				
Piona coccinea (Koch)							+					
Piona stjördalensis (Thor)							+					
Piona variabilis (Koch)							+					
Diplodontus scapularis Dugès								+				

(1) For relevés see van Vierssen and Verhoeven (1982).

Other species. In Table XVIII the species belonging to other groups are given. *Gammarus duebeni*, *Gammarus zaddachi*, *Pungitius pungitius* and *Gasterosteus aculeatus* are found frequently. It is obvious that a number of species are only found in the A6 community type. The number of species found in the isolated pools (A9 community type) is low.

Camargue (France)

In Table XIX the species composition of the three sampling stations in the Camargue is given. It is striking that there are many species which occur in only one of these three. The Insecta form up to 83% of the total species composition (see Table XII). According to the salinity, these habitats are

TABLE XVIII

Distribution of fauna in The Netherlands

Table/No. relevé	V 1	VI 4	VI 5	VI 7	V 2	V 4	V 5	IV 5	VI 36	VI 29	VI 31	(1)
Classification:	A6	A7	A7	A7	A7	A7	A7	A7	A8	A7 A9	A7 A9	A9
Pungitius pungitius (L.)	+	+	+	+	+	+	+	+	+	+	+	+
Gammarus duebeni Lilljeborg	+	+		+	+	+	+	+	+			
Gammarus zaddachi Sexton	+	+		+	+	+	+	+	+			
Gasterosteus aculeatus (L.)	+	+		+	+	+	+	+	+			
Neomysis integer (Leach)	+	+			+	+	+					
Palaemonetes varians (Leach)	+				+	+	+					
Gammarus tigrinus Sexton		+			+	+	+					
Helobdella stagnalis (L.)		+			+	+						+
Theromyzon tessulatum (Müller)		+			+	+	+					
Glossiphonia heteroclita (L.)		+				+	+					
Ischnura elegans (van der L.)		+			+	+						+
Limnodrilus hoffmeisteri Clap.					+	+	+	+				
Cloeon dipterum (L.)		+					+					+
Caenis robusta Eaton		+				+	+					
Potamothrix cf *hammoniensis* (Mich.)						+		+				+
Oecetis furva (Rambur)					+	+						
Limnephilus lunatus Curtis	+						+					
Erpobdella octoculata (L.)		+										+
Proasellus meridianus Racovitza		+				+						
Carassius carassius (L.)		+										
Cataclysta lemnata (L.)					+	+						
Polydora ciliata Johnston												
Nereis diversicolor (O.F. Müll.)	+											
Stratiomys sp.	+											
Gammarus salinus (Spooner)	+			+								
Sphaeroma hookeri Leach	+											
Electra crustulenta (Pallas)	+											
Anguilla anguilla (L.)	+											
Pomatoschistus microps (Kroyer)	+											
Piscicola geometra (L.)		+										
Dugesia lugubris (Schmidt)		+										
Argulus foliaceus L.		+										
Abramis brama (L.)		+										
Dendrocoelum lacteum (Müller)						+						
Polycelis nigra (Müller)						+						
Tubifex costatus (Clap.)	+											
Limnodrilus sp.												+
Limnodrilus profundicola (Verr.)								+				
Bufo bufo L.												+
Agraylea multipunctata Curtis							+					

(1) For relevé: van Vierssen and Verhoeven (1982).

TABLE XIX

Distribution of fauna in the Camargue (France)

Sampling station:	1	2	3
Community type:	A10—A11		
Plea leachi Mc.Greg. & Kirk	+	+	+
Lymnaea peregra (Müller)	+	+	+
Physa fontinalis (L.)	+	+	+
Gammarus plumicornis Costa	+	+	+
Berosus affinis Brullé	+	+	+
Chironomus plumosus/annularius	+	+	+
Planorbis carinatus Müller	+	+	
Asellus aquaticus L.	+	+	
Coenagrion mercuriale (Charp.)	+	+	
Naucoris maculatus F.	+	+	
Helochares lividus Forst.	+	+	
Ceratopogonidae	+	+	
Gambusia affinis (Baird & Girard)	+	+	
Chironomus thummi/halophilus		+	+
Polypedilum aberrans Chern.		+	+
Notonecta viridis Delc.	+		+
Procladius sp.	+		+
Coenagrion scitulum (Rambur)	+		
Micronecta meridionalis (Costa)	+		
Sigara dorsalis (Leach)	+		
Glyptotendipes sp.	+		
Polypedilum gr. *nubeculosum*	+		
Cyprinus carpio (L.)	+		
Gasterosteus aculeatus (L.)	+		
Bithynia tentaculata (L.)		+	
Pseudamnicola anatina Draparnaud		+	
Crocothemus erythrea Brullé		+	
Enochrus quadripunctatus Herbst		+	
Enochrus testaceus Fabr.		+	
Tanytarsus sp.		+	
Aeschna mixta Latreille			+
Leucorrhina pectoralis (Charp.)			+
Libellula depressa L.			+
Sigara stagnalis (Leach)			+
Agabus conspersus Marsh.			+
Coelambus impressopunctatus (Schall.)			+
Colymbetes fuscus (L.)			+
Dryops sp.			+
Haliplus cf *guttatus* Aubé			+
Haliplus lineatocollis Marsh.			+
Laccophilus minutus (L.)			+
Cricotopus ornatus (Meigen)			+
Psectrocladius sordidellus (Zetterstedt)			+
Rana esculenta L.			+

brackish (2.7‰ S, 1.8‰ S and 1.2‰ S, respectively), but freshwater species dominate (88% of the species composition). The temporary character of these habitats probably stimulates the occurrence of quick colonizers with a short residence time.

Classification

A classification will be made now on the basis of the fauna composition as given above for the different areas in western Europe. Only some general thoughts with respect to the standing and running freshwater communities will be given because not enough data could be collected in the given time.

Brackish water in the Baltic area

(a) Communities in rather stable chlorinity conditions of 2.5—3.5‰ on sandy substrates and on exposed shores. The fauna consists of a large number of species (35). The Crustacea and Mollusca are well represented (35 and 23% respectively). A large number of the species are euryhaline marine (23%) and brackish (23%). This fauna community often coincides with the A2 community type.

(b) Communities with brackishwater species as given under (a). Due to the influence of the nearby shore more aquatic life stages of land insects are present than in (a). The species number is in the same order of magnitude as in (a). This fauna community often coincides with the A1 and A3 community types.

Brackish water in The Netherlands

(c) Communities in brackish water with maximum chlorinities of 5—6‰ and mean chlorinities of 3—3.5‰. The brackish water species form 31%, the euryhaline marine species 23% and the freshwater species 43% of the total. The Insecta are well represented (43% of the species), followed quantitatively by the Crustacea (17%). *Potamopyrgus jenkinsi* and *Hydrobia ventrosa* are often found together and this species combination is very characteristic for this community type. The total number of species is 35. This fauna community often coincides with the A6 community type.

(d) Communities in brackish water with maximum chlorinities in summer of 5‰ and mean summer chlorinities between 0.5 and 3—3.5‰. The fauna consists largely of freshwater species (96%) with a few brackish-water species. The Insecta are dominant (59%), followed by the Mollusca (12%). The total number of species is between 14—70. Characteristic species are *Hygrotus inequalis* (dominant), *Laccobius minutus* (frequent), *Noterus clavicornis* (frequent) and *Laccobius biguttatus* (frequent). The combination of *Lymnaea peregra*, *Potamopyrgus jenkinsi*, *Lymnaea palustris* and *Planorbis planorbis* is characteristic for this community type. *Sigara lateralis*, *Sigara striata*, *Corixa punctata*, *Sigara stagnalis* and *Corixa affinis* occur frequently. This fauna community often coincides with the A7 and A8 community types.

(e) Communities in isolated, temporarily dry habitats with summer chlor-

inities of 3‰ and a minimum of 0.70‰. Most of the species are freshwater species (97%). Insecta occur in large numbers (76% of the species). *Coelambus confluens* is characteristic. Due to the frequent drying-out of the habitats and the occasionally high chlorinities the number of Mollusca is very low. The fauna consists of a rather small number of species (7—30) and this community often coincides with the A9 community type.

Brackish waters in the Camargue (France)

Only one community type has been distinguished. As a consequence of the drying-out of the habitats at different times in the season, a permanent presence of aquatic species is impossible. When such habitats are filled with water, a quick colonization occurs.

(f) Communities in temporary, brackish habitats. The number of species is rather low (ca. 25). Euryhaline freshwater insects are dominant (83%). Most of these species spend only a very short time in these habitats as larvae or pupae. This fauna community often coincides with the A10 and A11 community types.

Stagnant freshwater communities

The aquatic fauna of the freshwater communities was not extensively studied. Some general tendencies were obvious, however. In the large lakes of central Europe (classification B4) the deeper zones of the littoral were rather poor in specimens. The fauna in small stagnant waters with *Z. palustris* ssp. *repens* (classification B1, B2, B3) is obviously not dependent on this inconspicuous plant. The accompanying macrophytes are usually more important to these organisms (Soszka, 1974, Magnopotamids; van der Velde, 1980, Nymphaeids). Hardly any animals were found in a monospecific vegetation of *Z. palustris* ssp. *repens*.

Running freshwater communities

The composition of the fauna in running waters is of a totally different character to that of the fauna in standing water. The running water has such a large influence on the structure of this community type that a totally different community is present. Recently, Tolkamp (1981) described the community structure of macrofauna coenoses in relation to the different substrates of streams from a number of localities in The Netherlands. In the Mühlbach (W. Germany) it has been observed that *Z. palustris* ssp. *palustris* forms a good substrate for numerous animals (e.g., great numbers of Simulidae larvae) which live attached to these plants. In quiet parts of such habitats with emergent stands of macrophytes totally different animal species are found. Obviously a great number of subhabitats are formed by the different stream velocities. A special study is required.

Discussion and conclusions

It is obvious that a number of community types based on the aquatic

vegetation cannot be recognized with respect to the animal species composition The reason for this is that there are only a few animal species which live exclusively on one aquatic macrophyte species The factors which cause the distribution patterns of plants and those of animals are often totally different. Associations between animals and plants can be direct or indirect. The association of a plant and an animal is said to be direct when the occurrence of an animal is closely connected to the occurrence of a particular plant species, as with species-specific feeding relationships, and are said to be indirect when the animal is associated with plant characteristics that are not species-specific, e.g , the occurrence of an animal species on floating leaves or the co-existence of drought-resistant plants and animals in places that dry out.

Direct feeding relationships

No animal species restricted to specific aquatic macrophytes have been found in brackish water. At regular intervals plant material was checked to see whether there had been any mining by chironomidae larvae This was never observed, although it is a general phenomenon in aquatic macrophytes (Urban, 1975). In ecosystems with Nymphaeids, great losses of plant material were observed due to the feeding habits of several insect larvae (van der Velde, 1980).

Indirect feeding relationships

(1) *Lymnaea peregra* and *Planorbis planorbis* (and *Potamopyrgus jenkinsi* to a certain extent) feed on epiphytic algae The number of these gastropods is therefore partly dependent on the biomass of the aquatic macrophytes. Soszka (1975) states that *Lymnaea peregra* also feeds on other plant material. According to Calow (1970) this animal species feeds on filamentous algae

(2) Prey-catching occurs in the stands of aquatic macrophytes. The animals also shelter between the plants. These two functions are therefore coupled.

(3) The decomposition of plant material causes an increase of the detritus formation A certain number of species feeds on this material.

(4) Large amounts of fresh plant material in brackish waters are consumed by birds (Verhoeven, 1980b). Whether or not birds will feed on the (living) plants depends on the size of the habitat. In the regions where man's impact on the landscape is dominant, many habitats are no longer visited by birds because the surroundings are too frequently disturbed by man's activities (tourism, industry, urbanization, agriculture). A large amount of plant material is not consumed, probably due to the very unfavourable ratio between the size of these aquatic habitats and the multifunctional land area. It is difficult to establish whether direct feeding relationships between certain bird species and the aquatic macrophytes dominant in the studied ecosystems do in fact occur. No evidence supporting this assumption could be collected.

Plant material for non-food aims

Many Trichoptera larvae construct their cases from macrophyte tissue. *Limnephilus lunatus* has been observed to build cases from *Phragmites australis* leaves. *Oecetus furva* used *Zannichellia* seeds. The deposition of eggs on leaves of *Zannichellia* (and on aquatic plants in general) by Coleoptera, Heteroptera (Savage, 1979), Mollusca and Hydrachnellae has been frequently observed. Pupae of *Hydrellia* and *Ephydra* have often been seen attached to leaves of *Zannichellia* and *Potamogeton* species (in general on parvopotamids). In the Baltic area larvae and pupae of *Macroplea mutica* live attached to roots of *Z. major* and *Z. palustris* ssp. *repens* (Muus, 1967; Verhoeven, 1980a).

These relationships are not very intimate. They do not result in a clear association of animal and plant species. It is much more important to the different species whether the habitat dries out or has a fluctuating chlorinity. Some information with respect to the chlorinity-tolerance limits of animal species is given by Lindberg (1937, Finland), Seiffert (1938, Greifswalder Bodden, W. Germany), Jaeckel (1960, W. Germany), den Hartog (1964, The Netherlands), Soszka (1968, Poland), van Vierssen and Verhoeven (1978, 1982, The Netherlands) and Verhoeven (1980a, France).

The fauna communities co-existing with the A7—A8 macrophyte communities show the highest species number (see Table XII). The lowest number of species has been found in the A9 community. When comparing the results of this study with the results of Verhoeven (1980a), who studied similarly structured *Ruppia* communities, the following can be concluded: in the Baltic a larger number of animal species was found in the *Zannichellia*-dominated systems than in the *Ruppia*-dominated systems. This is probably partly due to the fact that for this study sampling took place three times whereas Verhoeven (1980a) was only able to sample once. In parts of *Z. palustris* ssp. *repens* stands a rather large number of freshwater species were collected. The distance to the shore is also very important. When this distance is short (as it is in a number of *Z. palustris* ssp. *repens* stands) aquatic stages of land insects easily colonize these habitats.

The maximum species number in communities with *Ruppia cirrhosa* and *Ruppia maritima* in The Netherlands was about the same as in the A6 and A9 community types. In general the freshwater Insecta dominate the stands with *Z. pedunculata*. The *Ruppia* communities are characterized by brackish-water animals.

In the Camargue the species number of the *Ruppia* and *Zannichellia*-dominated ecosystems is about the same. The latter are characterized by freshwater animals and the former by true brackish-water species. According to the species composition a large number of the communities with *Zannichellia* in The Netherlands and the Camargue are freshwater communities, although they are brackish according to the salinity data.

As was also discussed in pp. 112—113, small brackish habitats which dry out temporarily are considered to present different habitats (or subhabitats)

in one season. In spite of a rather high maximum chlorinity, there are certain periods in the year when because of the refilling by rainwater such a habitat is fresh. The salts need some time to redissolve and up to the moment this process results in high chlorinities numerous freshwater insects (e.g., chironomidae-larvae) can have completed their life-cycle. Therefore in a whole growing-season the number of species observed in such localities will probably increase because different species in fact inhabit the same place at different times.

Summarizing the results it is obvious that the *Z. pedunculata*-dominated communities are freshwater communities with at least the same number of species as the *Ruppia*-dominated ecosystems. In many instances more species are present. The Insecta dominate these communities and, because of the often very short life-cycle of these animals, even very brief suitable periods can be used to complete them.

When a number of isolated pools with a low chlorinity appeared to be inhabited by only a very few species this was clearly caused by the time it takes to colonize such a habitat. It is therefore not only the chlorinity regime that can cause a low species number in a community but also such factors as the size of the habitat (whether it dries out completely or not), the number of similar habitats in the surrounding area from which recolonization is possible after a dried-out habitat has become refilled with rainwater (see also pp. 105—110), or the final chlorinity reached before the habitat becomes completely dry (certain drought-resistant life-stages could be damaged by a high chlorinity).

The fact that the influence of a single factor on the species composition is so difficult to establish makes it very difficult to draw firm conclusions on the community level. One thing is obvious, however; since there are very few relationships between plants and animals the factors listed above are the most important ones. An additional difficulty, however, is the influence of man on the processes which determine the general characteristics of a habitat. Because the management (water regime) is often very different from year to year, many habitats have very unpredictable characteristics. This often results in a setback with respect to the species number after a sudden change in major environmental factors (such as the chlorinity) and a renewed process of colonization and settlement with its consequently low species number.

QUANTITATIVE ASPECTS OF FAUNA AND VEGETATION

Apart from the qualitative species composition of the fauna, the quantitative aspects of the *Zannichellia*-dominated communities have been studied in some selected localities. Because only few samples were collected within one year, no production figures can be presented but only a survey of the standing stocks as sampled at different moments in the season. These figures may, however, give some idea of the productivity of the different community types.

Material and methods

During the growing season of 1978, a quantitative sampling programme was carried out in a number of habitats in The Netherlands. These habitats are a small selection from the habitats qualitatively studied for the preceeding section on fauna species. In 1980 brackish communities in the Gulf of Finland (Tvärminne) and the Camargue (France) were quantitatively studied. Three different areas were chosen for the sampling programme in The Netherlands; Terschelling, the Ilperveld and Zeeuws-Vlaanderen. In Zeeuws-Vlaanderen, a temporary pool with a vegetation of *Z. pedunculata* and *Ranunculus baudotii* was sampled (community type A9; number 1). In The Ilperveld (peat substrate, brackish relicts from the time before the Zuiderzee was closed in 1932) a brackish ditch was studied (community type A7, number 7, Table IV, locality 3). Most samples were taken in brackish ditches on the island of Terschelling. Here, four brackish ditches were sampled with macrophyte stands belonging to the A7—A8 community types (numbers 2, 3, 4, 5. The localities 3, 4, 5,coincide with the relevés 3, 4, 5 in Table V. The other sampling stations on Terschelling are not represented by relevés in Table V because they were not visited in 1977) and two ditches with freshwater macrophytes (e.g., *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Potamogeton natans*, numbers 6, 8) for comparison.

In Finland (Tvärminne) two contrasting communities, one with *Z. palustris* ssp. *repens* (community type A1, Table II, locality 8) and the other with *Z. major* (community type A2, Table II, locality 6) were sampled. The sampling station of *Z. palustris* ssp. *repens* was situated in a relatively sheltered bay. In contrast to this, the sampling station of *Z. major* was located in rather turbulent water near an exposed shore.

In the Camargue (France), three sampling stations with A10—A11 communities were studied. Samples were taken once from two brackish marshes (Salin de Giraud, Le Paradis) and from a brackish ditch (Salin de Badon). In all these localities five replicate samples were taken to gain insight into the quantitative aspects of the communities. In general samples were taken at three different times in the growing season at one sampling station.

Whether a sample was representative for the community or not was answered by adding up the counts from the replicate samples in various combinations and then constructing curves to indicate the relationship between the number of species caught and the area sampled.

The fauna which inhabits the phytal zone was sampled by means of metal cylinders with a width of 30 cm and of various heights. The height of the cylinder was chosen according to the depth of the sampling station. In the waters of the Gulf of Finland a different sampler with a width of 18 cm was used (see Finnish IBP-PM Group, 1969). With both sampler types the top 10 cm of the sediment was included in the sample to collect the benthic (in-)fauna. When sampling, the sampler was placed in the vegetation without disturbing the fauna. Because of the very small size of the habitats this

method appeared to be very useful. The animals were removed from the metal cylinder with a large spoon.

All samples were stored under cold conditions (4°C). After the fauna had been removed from the cylinder the aquatic macrophytes were collected (including the subterranean plant parts). All organisms were preserved in 10% formalin buffered by hexamine (Lappalainen and Kangas, 1975). Because weight loss is known to occur due to storage (Donald and Paterson, 1977; Lappalainen et al., 1977; Wiederholm and Erikson, 1977; Landahl and Nagell, 1978), the ash-free dry weights were assessed as soon as possible. The ash-free dry weights of the animals were determined after subsequent drying (24 h, 105°C) and ashing (4 h, 550°C).

To compare the results, the diversity index of Shannon—Weaver ($H' = -p_i \ln p_i$ in which $p_i = n_i/N$ is the share of the number of animals of species i in the total number of animals, see Pielou, 1966) was calculated. As an additional index the 'evenness" ($J' = H'/\ln S$, in which S is the number of species) was calculated. Comparisons of the quantitative samples were also carried out by calculating the Biological Index and the Percentage Similarity according to Goodall (1973). The Biological Index indicates the importance of single animal species. This index is calculated by awarding the five most frequently occurring species in the samples the numbers one to five according to frequency. After summing up the number of points given to a species in the various samples, the quantitative importance of the different species can be expressed for one sampling station.

The sampling programme of a brackish polder reservoir with an A6 community (very rare in The Netherlands) had to be cancelled because of an unexpected and illegal treatment with herbicides.

Results

In Figs. 17—25 the quantitative data as collected in The Netherlands are summarized. In Figs. 17 and 18 the quantitative results from a brackish pool (community type A9) in Zeeuws-Vlaanderen have been summarized. In this community type the Mollusca and Chironomidae produce the largest part of the biomass. *Potamopyrgus jenkinsi* clearly has two generations in one year and *Lymnaea peregra* only one. In spring numerous *Bufo bufo* larvae are found in this pool. The biomass of the animals starts to decrease in the beginning of October but until the end of December it remains higher than in August.

In Figs. 19—23 the results from the brackish ditches on the island of Terschelling are shown. Figure 24 gives the results from two freshwater communities which serve as a reference. These two ditches are situated very near the brackish water ditches so a good comparison is possible. From Figs. 19—23 it follows that in the brackish communities with mixed vegetation stands of *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* the Chironomidae larvae occur in relatively great numbers and that they produce a

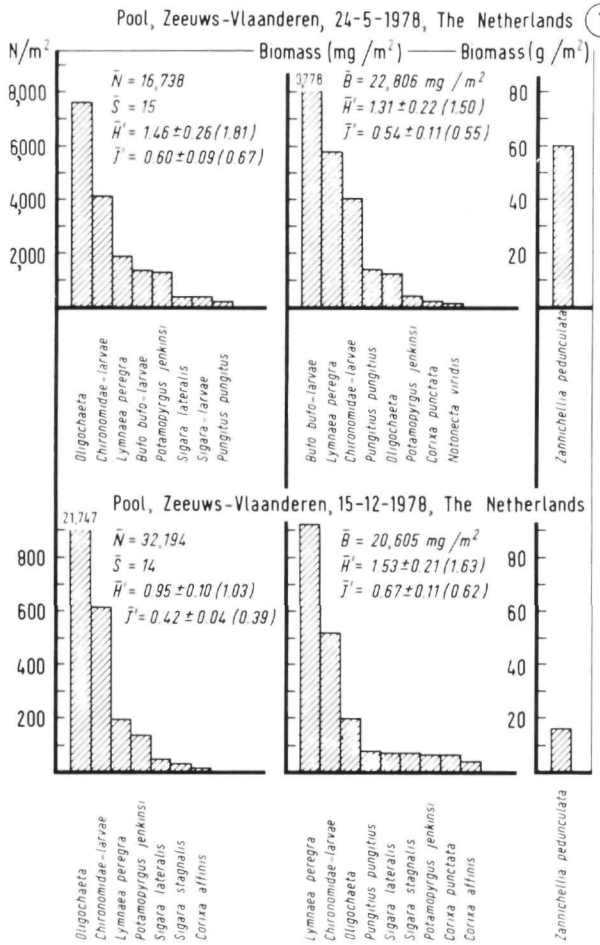

Fig. 17. Quantitative results of the sampling programme in station 1 (community type A9), Zeeuws-Vlaanderen, The Netherlands. $\bar{N}$ = mean number of organisms/m²; $\bar{S}$ = mean number of specimens in one sample; $\bar{H}'$ = mean Shannon—Weaver index (±S.D.); $\bar{J}'$ = mean Evenness (±S.D.); $\bar{B}'$ = mean biomass of the fauna/m². The figures in parentheses (for H' and J') represent the H' and J' figures calculated for the sample comprising all five subsamples.

large biomass. In many instances, *Limnodrilus hoffmeisteri* and *Potamothrix hammoniensis* (Oligochaeta) also occur in considerable numbers, especially somewhat later in the season. *Lymnaea peregra*, *Planorbis planorbis* and *Potamopyrgus jenkinsi* are frequently found. The number of animals steadily increases from the beginning of the growing season up to the autumn. This is caused by the increasing number of Chironomidae larvae and Oligochaeta. The total biomass also steadily increases. Fig. 23 gives the distribution of the number of animals and their biomass over the different species in sampling

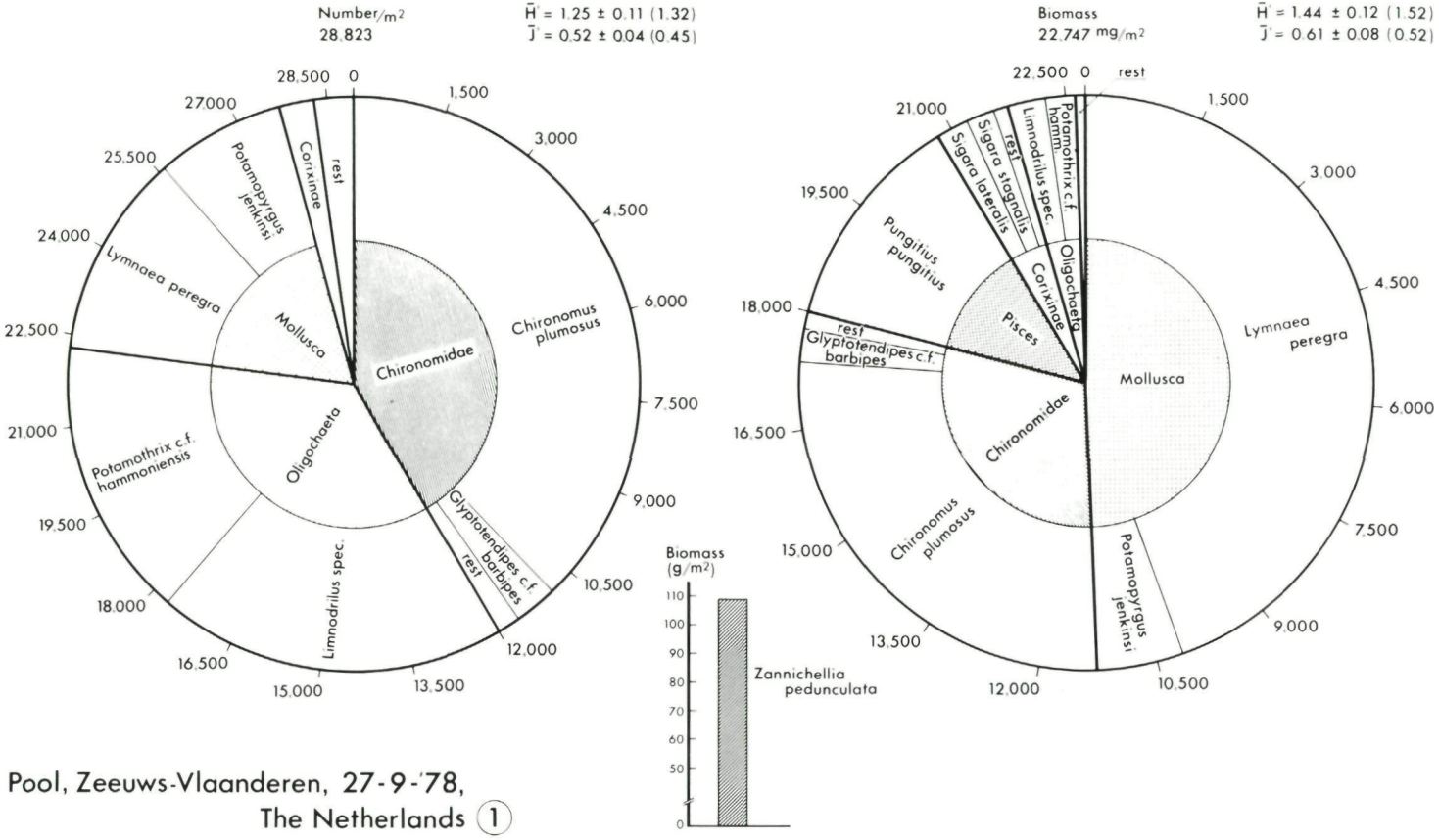

Fig. 18. Relative quantitative importance of different fauna groups in station 1 (community type A9), Zeeuws-Vlaanderen. Symbols: see Fig. 17.

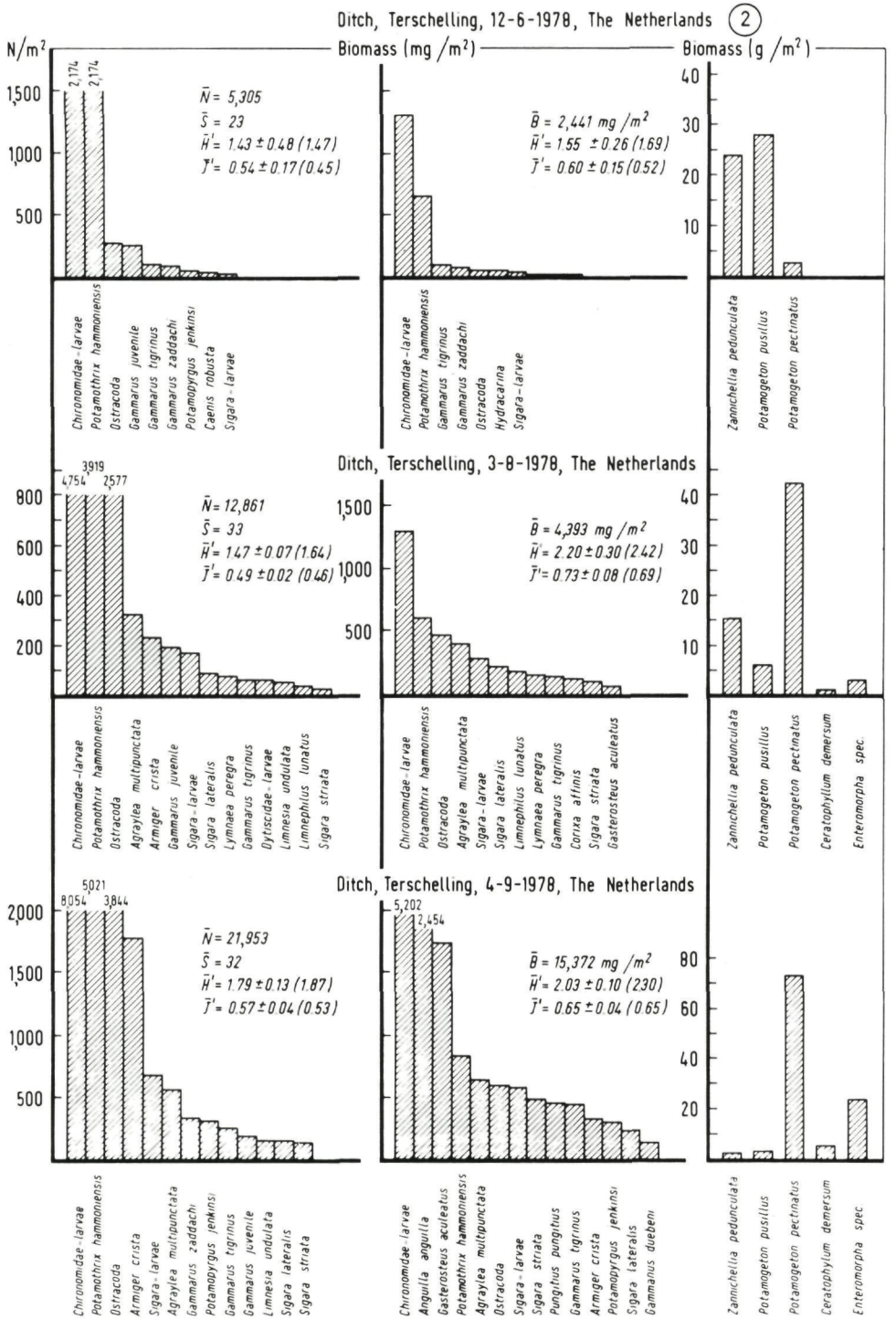

Fig. 19. Quantitative results of the sampling programme in station 2 (community type A7), Terschelling, The Netherlands. Symbols: see Fig. 17.

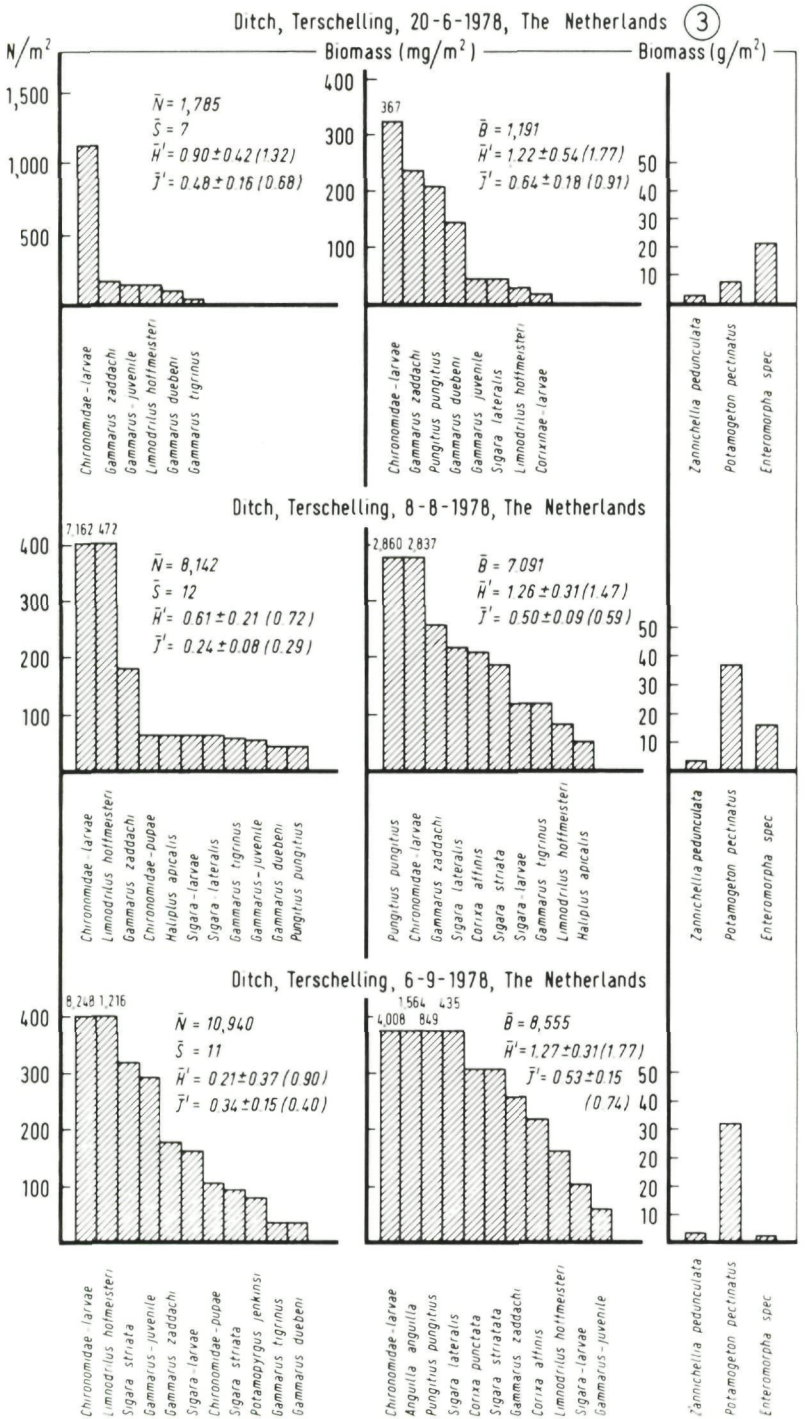

Fig. 20. Quantitative results of the sampling programme in station 3 (community type A7), Terschelling, The Netherlands. Symbols: see Fig. 17.

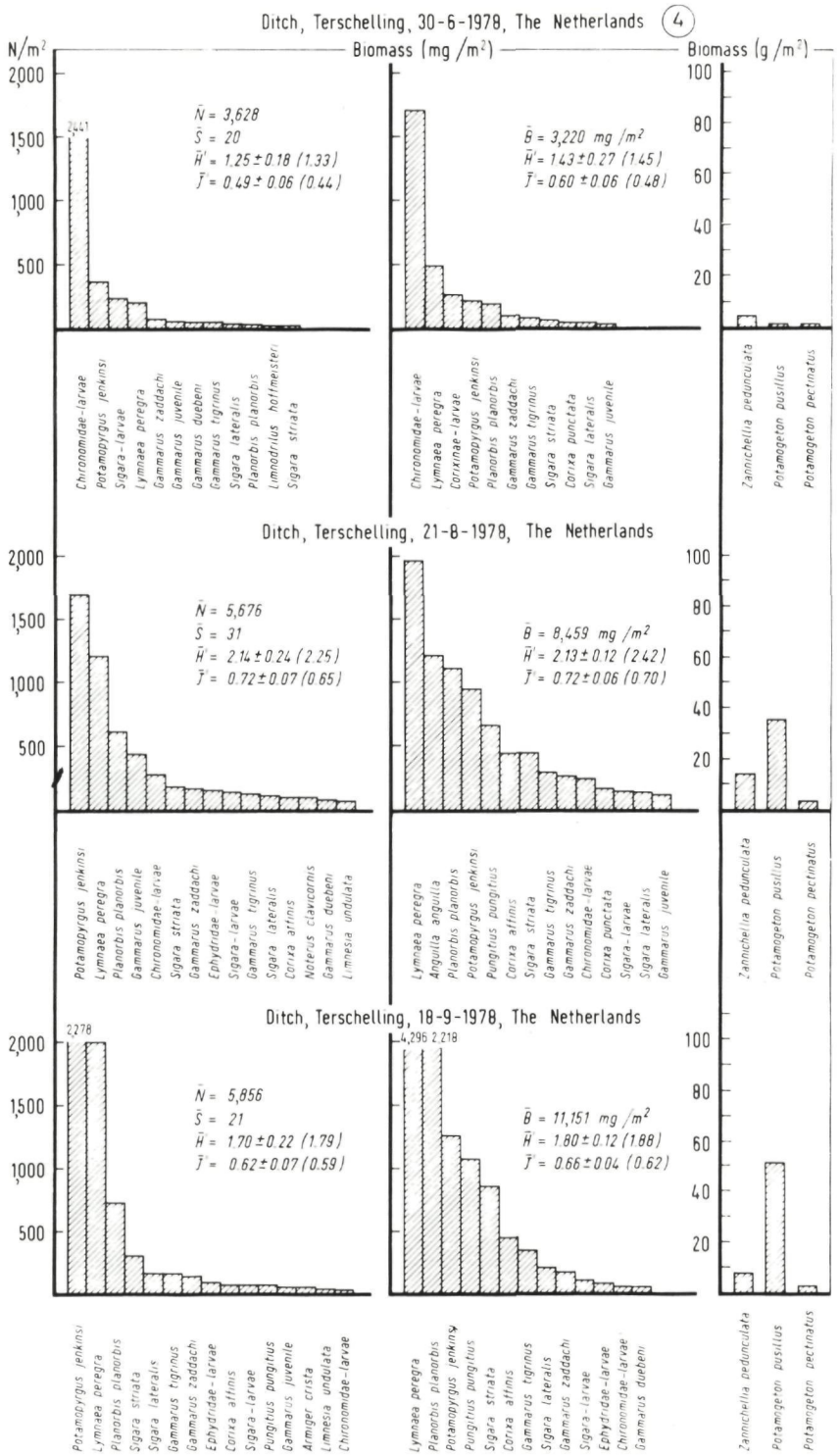

Fig. 21. Quantitative results of the sampling programme in station 4 (community type A7), Terschelling, The Netherlands. Symbols: see Fig. 17.

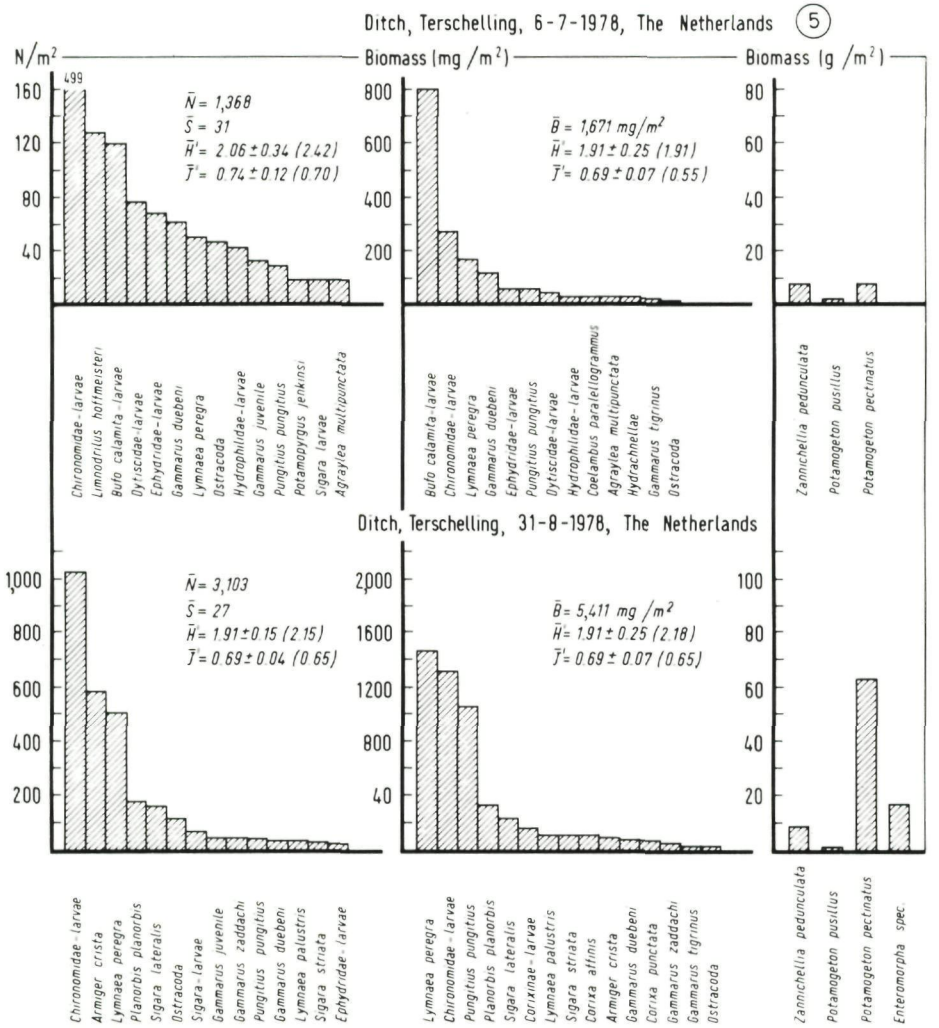

Fig. 22. Quantitative results of the sampling programme in station 5 (community type A7), Terschelling, The Netherlands. Symbols: see Fig. 17.

station 5. This figure offers a good impression of such a distribution for one of the most characteristic community types with *Z. pedunculata*, viz. the A7 community type. The Diptera-larvae and the Mollusca are very important. *Armiger crista* occurs in relatively large numbers but its biomass is, of course, not very important.

In Fig. 24 the quantitative results of the sampling programme in the freshwater ditches have been summarized. *Anisus vortex* and *Planorbis planorbis* are important species. A larger number of Mollusca species is present than in

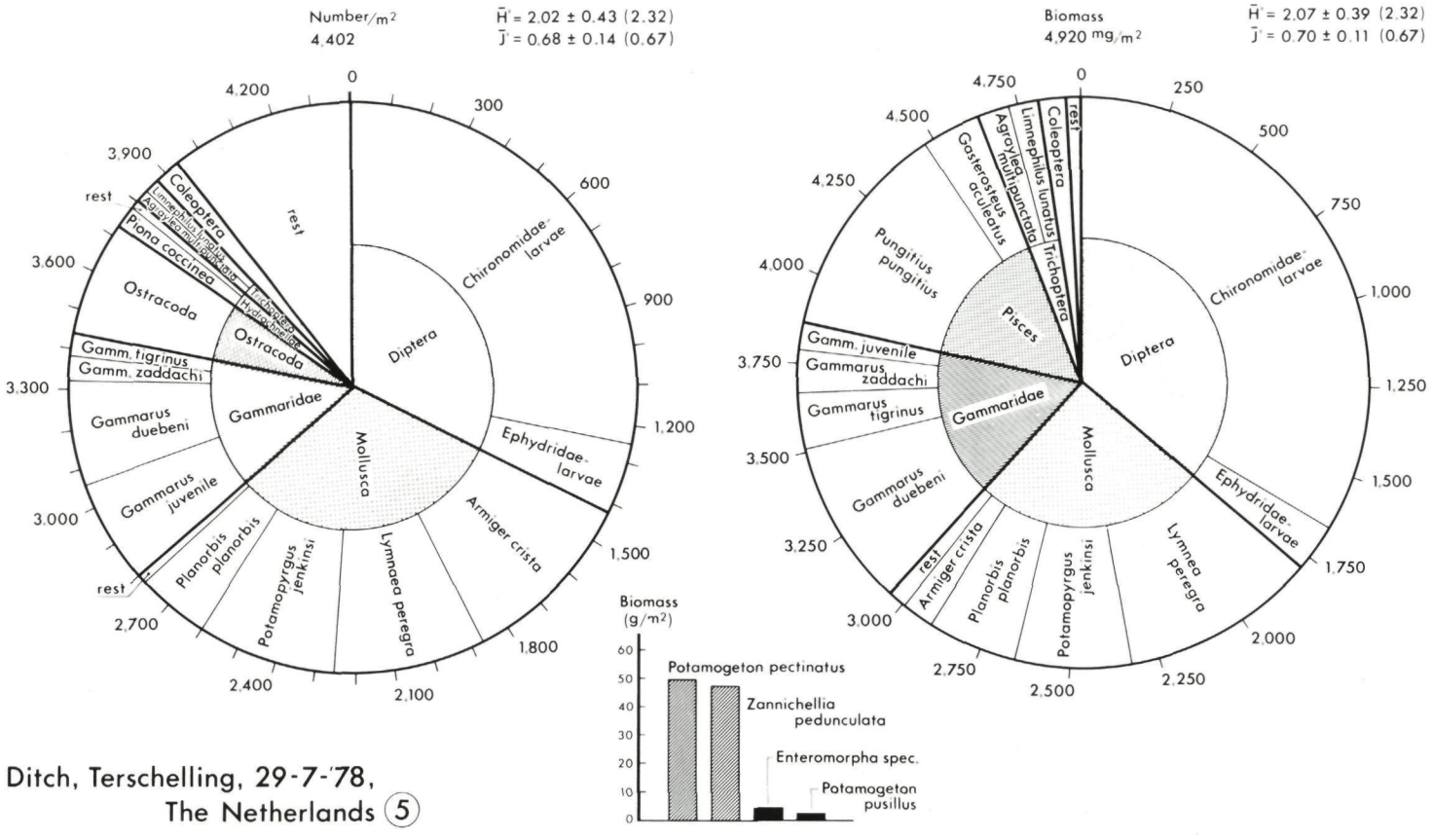

Fig. 23. Relative quantitative importance of different fauna groups in station 5 (community type A7), Terschelling, The Netherlands. Symbols: see Fig. 17.

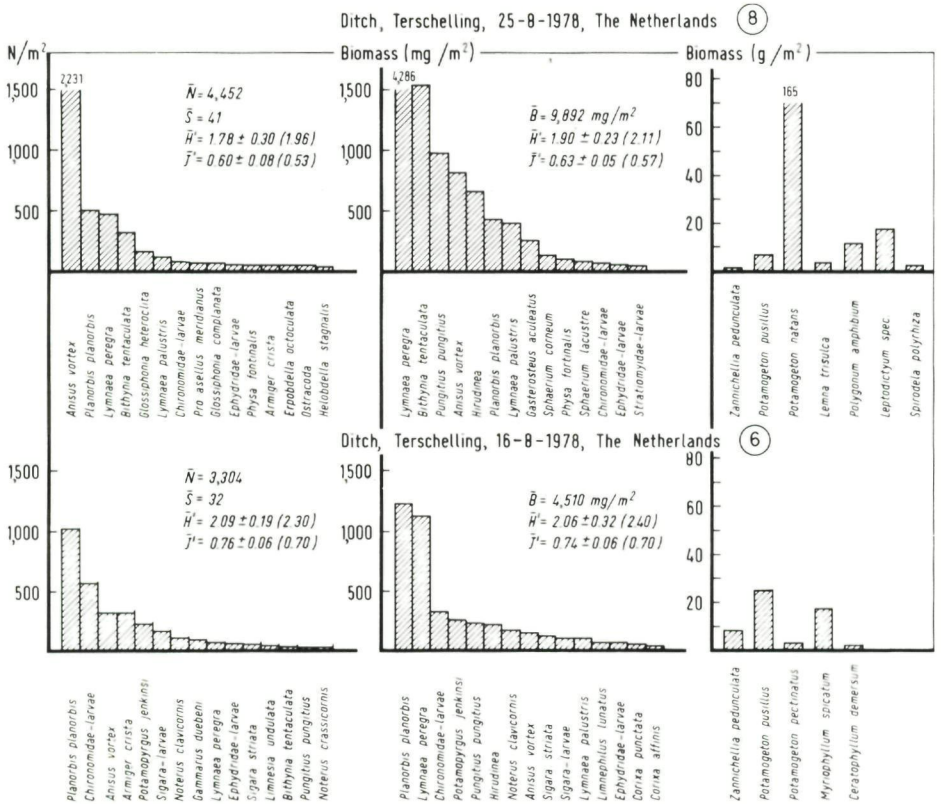

Fig. 24. Quantitative results of the sampling programme in the stations 6 (community type A8/freshwater ecosystem) and 8 (freshwater ecosystem), Terschelling, The Netherlands. Symbols: see Fig. 17.

the *Zannichellia*-dominated coenoses. It is obvious that the Hirudinea is also an important group. A relatively large number of species occurs in small amounts.

In Fig. 25 the results of the quantitative sampling programme in the Ilperveld are illustrated. Although the macrophyte species composition resembles that of the brackish ditches on Terschelling, the number of animals per species and their biomass is rather different. Species such as *Cymatia coleoptrata*, *Bithynia tentaculata*, *Valvata piscinalis* and *Sigara striata* do not occur in the communities on Terschelling. In the Ilperveld they obviously migrate from the surrounding freshwater habitats into the communities with *Zannichellia*. This is partly because the chlorinities have already decreased enormously during the last decades in this area (which started after the closure of the Zuiderzee). Some brackish waterplants obviously still manage to survive the competition with freshwater macrophytes and this suggests that the communities are brackish. The chlorinities are already so low, however, that

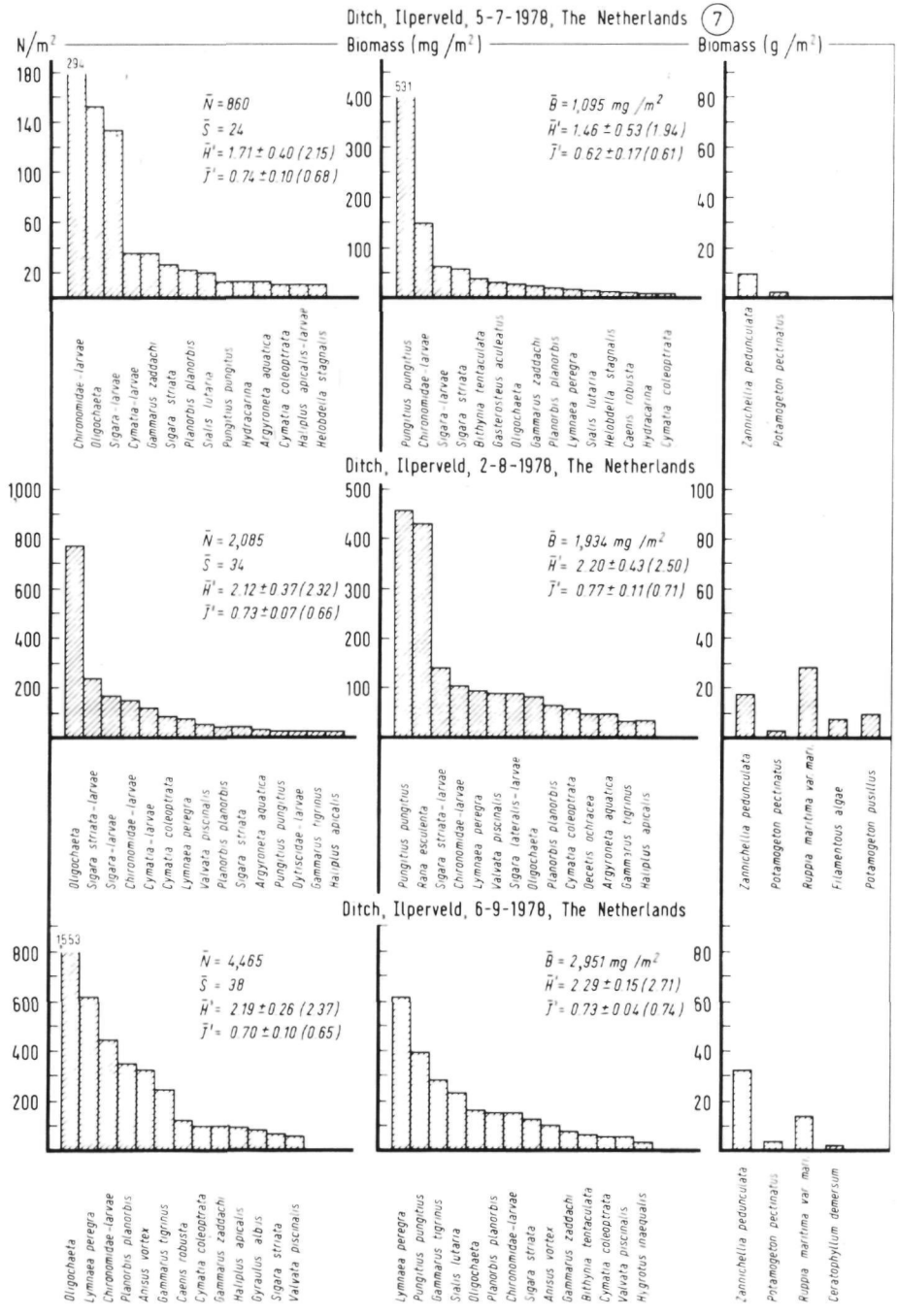

Fig. 25. Quantitative results of the sampling programme in station 7 (community type A7), Ilperveld, The Netherlands. Symbols: see Fig. 17.

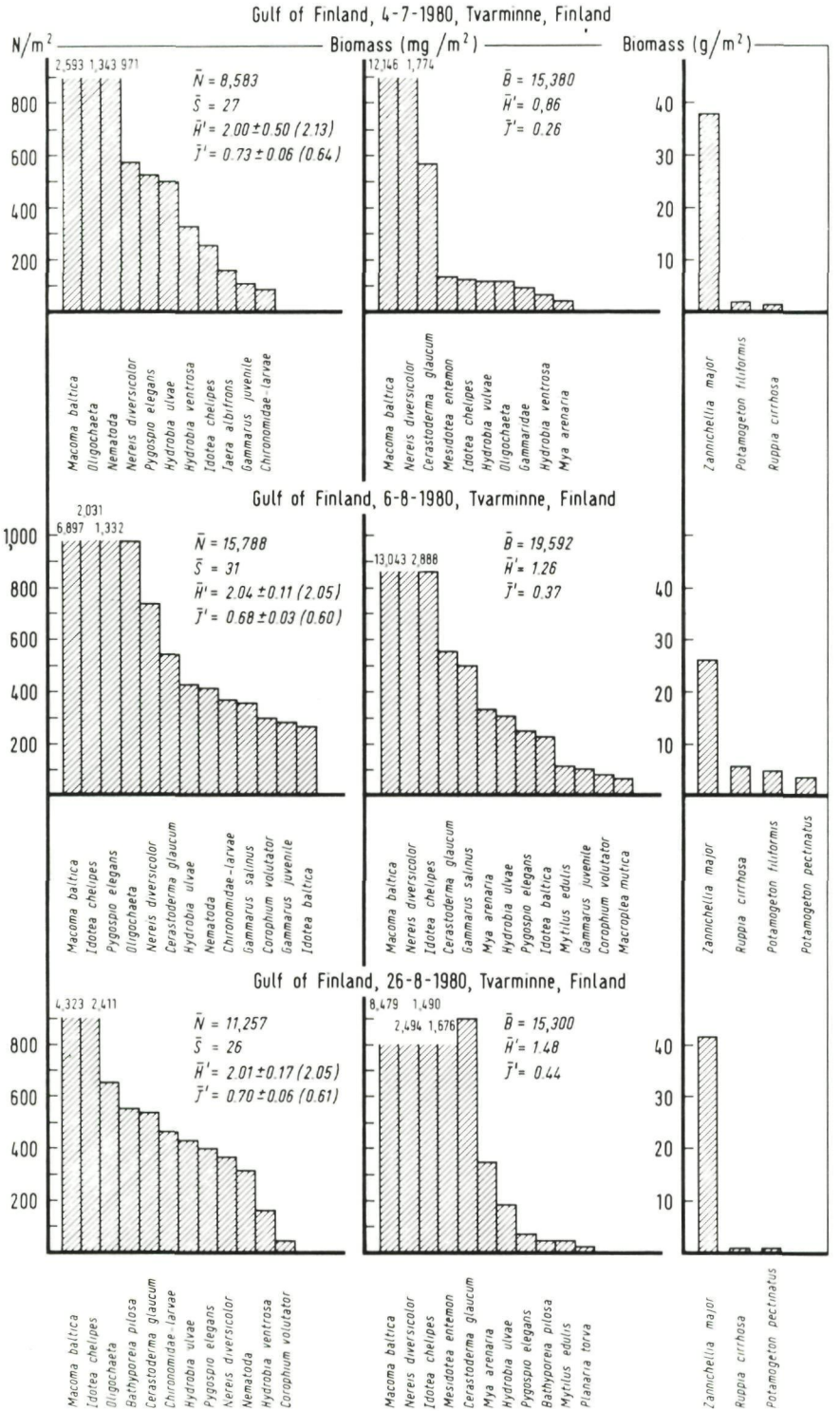

Fig. 26. Quantitative results of the sampling programme in the Tvärminne area (community type A2), Finland. Symbols: see Fig. 17.

freshwater animals do not have to cope with severe chlorinity stresses. Therefore the surrounding freshwater communities which outnumber the brackish-water communities, have a great influence on the latter.

In Figs. 26 and 27 the results of the sampling programme which was carried out in Tvärminne (Finland) are given. *Macoma baltica*, *Nereis diversicolor* and *Idotea chelipes* are quantitatively important species. The differences between the *Z. major*-dominated stands and the stands dominated by *Z. palustris* ssp. *repens* are due to species exclusively present in one of the two community types. The differences in Chironomid species composition are striking.

In Fig. 28 the results of the sampling in the Camargue (France) have been summarized. It is striking that the biomass is very low in the sampling stations. The number of species, however, is relatively large.

By means of the Biological Index and the Percentage Similarity it was tried to group the sampling stations from The Netherlands on a quantitative basis. From Fig. 29 it follows that the stations 1—3 show a rather low resemblance to the other sampling stations on a basis of Percentage Similarity (numbers). Stations 4—8 inclusive show a rather high internal similarity. The sampling stations 1, 2 and 3 represent the brackish community types (d) and (e) (see p. 130). The habitats can be characterized as rather exposed (large pool, wide canal or ditch). The stations 4—8 inclusive partly represent the same community types (4, 5, 7) but the habitats are characterized by their sheltered situation. Apparently this factor is very important. It causes larger differences between coenoses of the same community type than often exist between different types of communities. These differences are apparently caused by factors such as the quick and permanent colonization by freshwater organisms in a location where brackish habitats are outnumbered by freshwater habitats, e.g., in the Ilperveld. In small brackish habitats (small ditches with a width of less than a metre) the colonization by aquatic life stages of land insects in the emergent vegetation will have a relatively large effect on the species composition of the brackish community. In large brackish habitats this colonization will also occur but will be of less importance.

The distribution of the biomass over the different species gives rise to a somewhat different classification of the sampling stations. The similarities between the sampling stations on a basis of the percentage similarity are also illustrated in Fig. 29. When analyzing this figure it becomes obvious that subsequent sampling stations only differ slightly with respect to the distribution of the biomass over the different species. No clear, separate groups can be indicated. The high similarity between a freshwater ditch on Terschelling (sampling station 8) and a brackish pool (sampling station 1) is striking. This similarity is caused by the quantitative importance of *Lymnaea peregra* and *Pungitius pungitius* in both sampling stations.

In Table XX the biological indices for the sampling stations in The Netherlands have been summarized. In column (a) the total sum of the biological indices, as calculated for the separate sampling stations, is summarized. In column (b) this sum has been calculated for the sampling stations 1—5, which

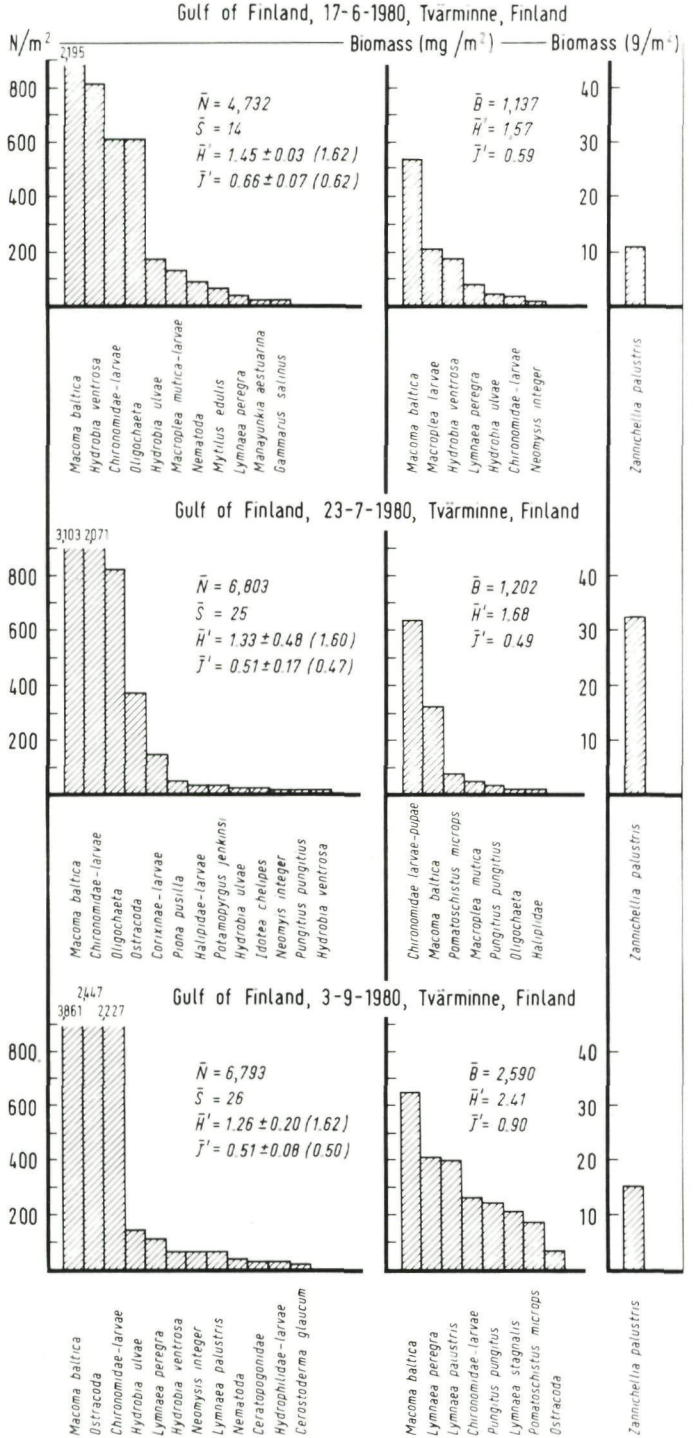

Fig. 27. Quantitative results of the sampling programme in the Tvärminne area (community type A1), Finland. Symbols: see Fig. 17.

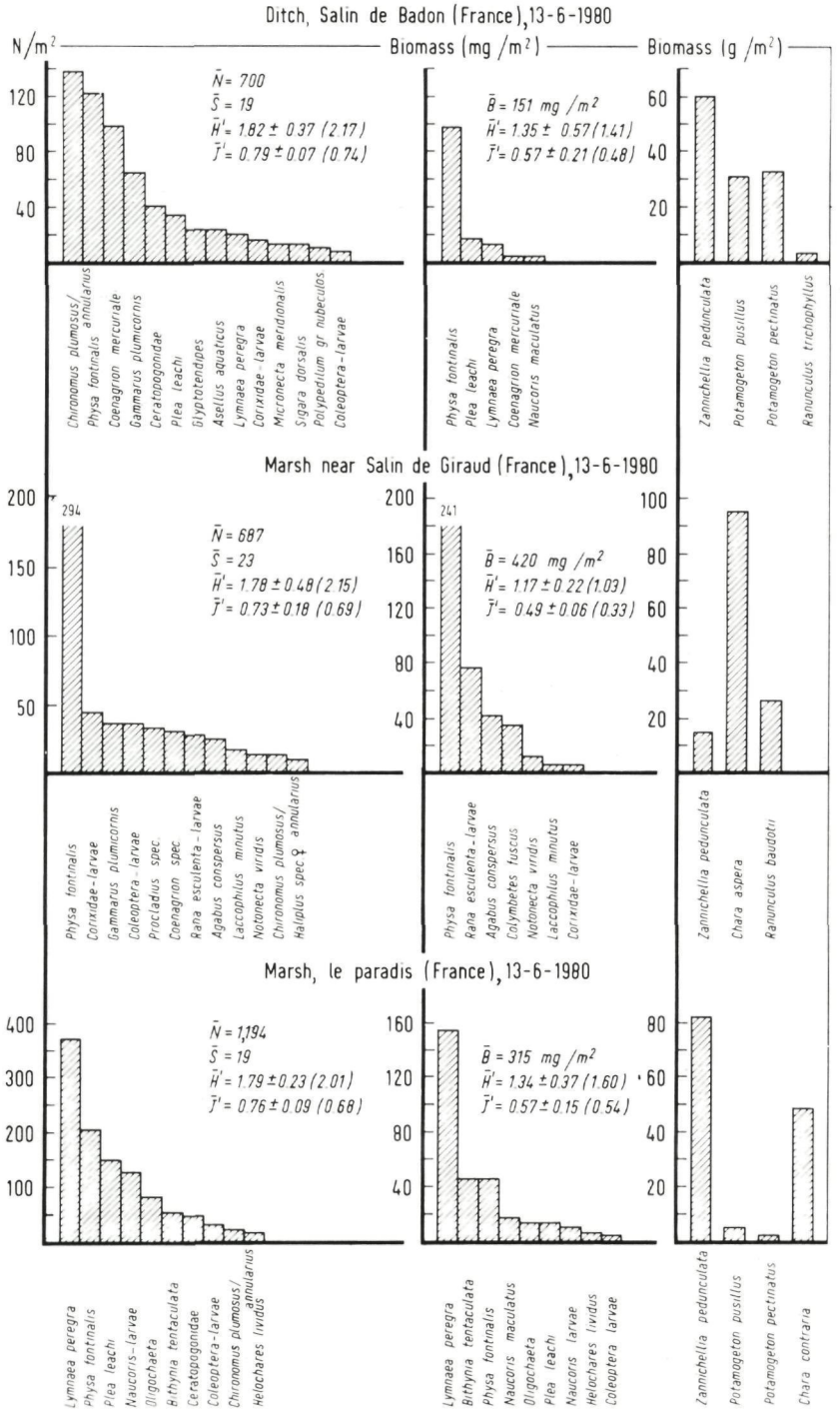

Fig. 28. Quantitative results of the sampling programme in the Camargue (community types A10, A11), France. Symbols: see Fig. 17.

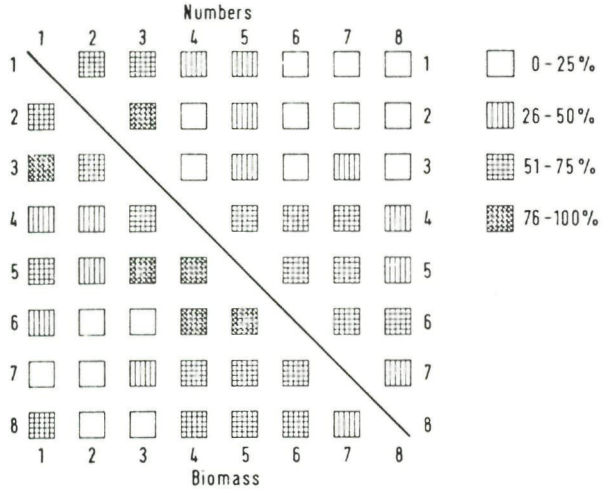

Fig. 29. Percentage Similarity of sampling stations in The Netherlands on the basis of the quantitative data (numbers and biomass). The numbers 1—8 refer to the numbers of the sampling stations given in the Figs. 17—25.

are the sampling stations with dominant stands of *Z. pedunculata* in brackish water. In these communities the Chironomidae larvae are most numerous, followed by *Lymnaea peregra* and *Planorbis planorbis*. The biomass of these species is also very important. *Pungitius pungitius* also has a relatively high share in the total biomass. The freshwater sampling stations (6,8) which were sampled as a reference show that *Anisus vortex* and *Planorbis planorbis* (numbers) are very numerous. *Lymnaea peregra* shows the highest biomass in these systems. The H′ indices which were calcualted for the different sampling stations are significantly and positively correlated with the J′ indices (rank correlation of Kendall, $P < 0.005$). This means that an increasing diversity is correlated with a more evenly distributed number of animal specimens over the various species. The H'_n and H'_b indices are in the same order of magnitude in The Netherlands. In the Baltic area, however, the H'_b indices are lower because of the quantitative (biomass) dominance of *Macoma baltica*.

In the Camargue the H'_n and H'_b indices are again of the same order of magnitude. The biomass of the accompanying macrophytes, as collected simultaneously with the fauna, is also given in Figs. 17—28. During the growing season relatively large standard deviations of the mean biomass were found for single plant species.

When calculating the standard deviation of the total biomass it was found that this deviation was relatively small. The standard deviation of the total biomass in mixed stands (with *Z. pedunculata*, *Potamogeton pectinatus* and *Potamogeton pusillus*) was about the same as in monospecific stands of *Z. pedunculata*. The largest biomass ever found for *Z. pedunculata* stands was 238 g ash-free dry weight/m² (sampling station 1), but very frequently biomasses of less than 100 g ash-free dry weight/m² were found. It has to be

TABLE XX

Survey of quantitative important species according to the Biological Index for the sampling stations in The Netherlands. Under a the results are given for the brackish waters (1—5) and under b for all sampling stations.

	Numbers								Total		Biomass								Total	
	1	2	3	4	5	6	7*	8	a	b	1	2	3	4	5	6	7*	8	a	b
Chironomidae-larvae	31	32	33	—	31	14	15	—	127	156	24	31	31	—	28	8	—	—	114	135
Lymnaea peregra	21	—	—	28	21	19	—	16	70	105	31	—	—	32	27	31	—	33	90	166
Planorbis planorbis	—	—	—	19	9	32	—	20	28	80	—	—	—	21	9	29	—	—	30	59
Anisus vortex	—	—	—	—	—	21	—	33	0	54	—	—	—	—	—	—	—	—	—	—
Pungitius pungitius	—	—	—	—	—	—	—	—	—	—	25	—	20	9	21	—	—	16	75	91
Sigara striata	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	23	—	9	32

Localities: 1 Pool Zeeuws-Vlaanderen, 23-8-'78 (Figs. 17, 18), 2 Ditch Terschelling, 4-9-'78 (Fig. 19), 3 Ditch Terschelling, 8-8-'78 (Fig. 20), 4 Ditch Terschelling, 21-8-'78 (Fig. 21), 5 Ditch Terschelling, 31-8-'78 (Figs. 22, 23), 6 Ditch Terschelling, 16-8-'78 (Fig. 24), 7 Ditch Ilperveld, 9-6-'78 (Fig. 25), 8 Ditch Terschelling, 8-8-'78 (Fig. 24).
*Station 7 is considered as a freshwater habitat because it is only a relict with slowly disappearing brackish characteristics.

remembered, however, that in mixed stands seasonal aspects are very important In different periods different species reach their maximum biomass. When adding up the different maximum biomasses of those species which grow in a habitat during one growing season, total biomasses of ±70 –±300 g ash-free dry weight/m^2 are normal (last figure originates from a mixed vegetation of *Z pedunculata* and *Ruppia maritima* var *maritima* which is not quantitatively described in this study).

Discussion and conclusions

When comparing the quantitative results as found in this study with those from the *Ruppia*-dominated ecosystems (Verhoeven, 1980a), the following is obvious from Table XXI.

In the Baltic no large differences exist. The H' indices are in the same order of magnitude In The Netherlands, however, the number of animals found in the *Zannichellia*-dominated communities is somewhat lower than in the *Ruppia* communities. In the latter there is a strong dominance of a relatively small number of species and this is reflected by a lower H'_n than in the *Zannichellia*-dominated communities The H'_b indices are also much lower in the *Ruppia* communities although the maximum biomass is of the same order of magnitude This means that in the *Ruppia*-dominated systems a few species are responsible for the largest part of the animal biomass.

In spite of the very low species number in the Camargue the H' indices are relatively high, in contrast to those calculated for the *Ruppia*-dominated communities. On a European scale it is obvious that the *Z pedunculata* communities in the Baltic, The Netherlands and the Camargue have almost the same H'_n indices The A9 community has the relatively lowest indices, which are about the same as the highest indices for the *Ruppia* communities (Baltic) Comparing the *Ruppia* communities in western Europe from north to south it is obvious that the H'_n indices become gradually lower. There are two different reasons for this.

In the first place, going from north to south the changing chlorinity regime in the *Ruppia* communities results in a less diverse community. The strong chlorinity fluctuations in southern Europe exclude a number of species which cannot be replaced by e g., freshwater insects because the lowest chlorinity in the season is still too high for these organisms. In the *Zannichellia*-dominated communities the situation is quite different. Although the maximum chlorinity in some communities may be too high for certain species, there is a certain period in the growing season when freshwater animals with a short life-cycle can colonize. Whereas the special environmental conditions in the *Ruppia* communities in southern latitudes emphasize the brackishwater characteristics, the local conditions add freshwater characteristics to the temporarily brackishwater characteristics in *Zannichellia*-dominated communities in these latitudes.

Secondly, there are almost no true brackish-water species, such as insects

TABLE XXI

Survey of quantitative parameters in brackish-water fauna communities

Area	Community type	Number of specimens	Biomass		
		$N \times 10^{-3}/m^2$	$B(mg) \times 10^{-3}/m^2$	H'_n	H'_b
Finland	A1—A3	4.7—15.8	1.1—19.5	1.26—2.13	0.86—2.4
	Ruppia species	1.9—18.6	—	1.33—2.12	—
The Netherlands	A6—A9	0.9—28.8	1.1—22.9	0.61—2.37	1.22—2.7
	Potamogeton natans-type	4.5	9.9	1.96	2.11
	Myriophyllum spicatum-type	3.3	4.5	2.30	2.40
	Ruppia species	2.3—43.8	1.6—22.9	0.96—1.50	0.26—0.9
France	A10—A11	0.7—1.2	0.15—0.42	1.78—2.17	1.17—1.6
	Ruppia species	2.3—12.2	1.1—7.0	0.13—1.45	0.41—1.2

The data concerning the *Ruppia*-dominated communities were quoted from Verhoeven (1980a).

with a short aquatic life stage, which only temporarily inhabit aquatic communities. In fact there are only a few such opportunistic brackish-water organisms. Plotting the number of species against the H'_n and H'_b indices for *Zannichellia*- and *Ruppia*-dominated communities it appears that *Zannichellia* communities with the same number of species as *Ruppia* communities generally have a lower H'_n. A *Ruppia* community with eight species has a H'_n of about 1.50. To reach a H'_n of 1.50 a *Z. pedunculata* community needs about 20 species. In the traject with a rather low species number (more stations with *Ruppia* than *Zannichellia*), an increase in the number results in a relatively large increase of the H'_n. In the traject in which *Z. pedunculata* communities usually occur with respect to their species number (20—35), an increase of the species number does not result in a very large increase of the H'_n. In the *Ruppia*-dominated systems a dominance of a single species occurs more frequently than in the *Zannichellia*-dominated ecosystems. These differences between the two ecosystem types are most likely caused by differences in the population dynamics of different taxonomical groups with different life-strategies rather than by differences directly related to the floristic composition or the brackish-water factor.

In *Ruppia* communities the population dynamics of the fauna are largely determined by the dynamics of established populations (Bivalvia, Gastropoda, Polychaeta). In *Z. pedunculata*-dominated communities the population dynamics are largely determined by the colonization rate of e.g., insects. Since a few species produce a relatively high biomass in *Ruppia*-dominated ecosystems and a change in the number of species obviously results in a relatively large change in the H'_n index, these systems are relatively unstable. The disappearance of one (quantitatively important) species is likely to result in totally different energetic pathways in these systems. Such large shocks are not likely to occur in *Z. pedunculata*-dominated systems because many more species are involved in those.

Compared with the freshwater reference systems (with *Potamogeton natans* and *Myriophyllum spicatum*, see Table XXI) it is obvious that the H'_n and H'_b are of the same order of magnitude as the maximum values found in the *Z. pedunculata*-dominated communities. The number of animals and their biomass are much lower, however.

As Verhoeven (1980a) already stated after comparison of his data with that in the literature, the brackish waters with *Ruppia* taxa are moderately productive with respect to their aquatic macrophyte production (maximum biomass 25—290 g ash-free dry weight/m^2). In the Baltic the maximum standing stock in *Zannichellia*-dominated communities was lower than in The Netherlands. For *Z. major* this maximum was about 40 g ash-free dry weight/m^2 and for *Z. palustris* ssp. *repens* about 30 g ash-free dry weight/m^2. Besides the relatively poor light conditions in these latitudes, wave action is considered to be partly responsible for these low figures. No exact data have been collected but, because of the rather exposed character of the habitats, some plant material will certainly be removed by wave action during the

growing season. In the small pools and ditches in The Netherlands this influence is negligible. Besides a longer growing season, the population takes advantage of a good start because rhizome parts which hibernated bud and guarantee a quick development. These relatively favourable conditions result in a maximum standing stock of about 250 g ash-free dry weight/m^2.

In the Camargue, a maximum standing stock of about 80 g ash-free dry weight/m^2 for *Z. pedunculata* is found. The rising chlorinity and the slow drying of the habitat early in the growing season often inhibit further growth. There are no large differences between these results and those from Verhoeven (1980b) for *Ruppia*-dominated communities.

The figures for seagrass ecosystems are considerably higher in western Europe (Sand-Jensen, 1975; Nienhuis and de Bree, 1977; Jacobs, 1979). An annual net production of more than 1500 g ash-free dry weight/m^2 is not unusual. When using the turnover ratios as given by Verhoeven (1980b) for the similarly structured *Ruppia* stands, the *Zannichellia*-dominated communities produce considerably less material than the *Zostera* communities. Many figures for freshwater macrophytes are much lower. Most data, however, represent maximum standing stocks. As Westlake (1975) summarizes, maximum standing stocks of up to 700 g ash-free dry weight/m^2 in freshwater ecosystems can be expected. It is very speculative to draw firm conclusions from these comparisons. The question to be raised is to what extent are the productivity characteristics of the communities with aquatic macrophytes determined by the characteristics of the habitat (nutrient levels, light conditions) and to what extent by the potential growth capacities of the various aquatic macrophytes.

The effect of competition between different aquatic macrophytes on the productivity of mixed vegetation stands has hardly been studied yet. The classification of aquatic communities on the basis of productivity characteristics should also contain such information besides information on the growth capacities of single plant species in relation to environmental conditions. Summarizing the quantitative (biomass and numbers), fauna and vegetation (biomass) characteristics the following is concluded.

(1) The maximum standing stock of *Zannichellia pedunculata* in western Europe is about 250 g ash-free dry weight/m^2. In the Baltic area a maximum of about 40 g ash-free dry weight/m^2 for *Z. major* and of about 30 g ash-free dry weight/m^2 for *Z. palustris* ssp. *repens* is found. These figures are in the same order of magnitude as found for the similarly structured *Ruppia* taxa.

(2) In the Baltic area *Macoma baltica*, *Nereis diversicolor*, *Idotea chelipes* and, in sheltered bays, Chironomidae larvae quantitatively characterize the *Zannichellia*-dominated communities. These communities can be characterized as brackish-water communities.

(3) In The Netherlands the *Z. pedunculata* communities are quantitatively characterized by freshwater taxa (Chironomidae, *Lymnaea peregra*). Compared with the brackish *Ruppia* communities, the *Zannichellia*-dominated communities are more diverse because more species are present in lower num-

bers. The *Zannichellia*-dominated communities are even more diverse with respect to the distribution of the biomass over the different species. Therefore, these communities are considered to be more balanced than the *Ruppia*-dominated communities and, according to the species composition, they can be considered as freshwater communities.

(4) In the Camargue, the diversity of the fauna in *Z. pedunculata*-dominated communities is relatively high. There are only few species present, with a low number of specimens. The biomass is very low because every year the habitats dry out completely and have to be colonized again. The communities can be characterized as freshwater ecosystems according to their species composition.

(5) There is no obvious relationship between the number of animals in the phytocoenoses and the biomass of the aquatic macrophytes.

GENERAL EVALUATION OF THE RESULTS

The distribution of *Zannichellia* taxa in western Europe can be well understood when considering the results of the autecological experiments with *Zannichellia* from Part I of this study (van Vierssen, 1982a). The germination ecology of the different *Zannichellia* taxa is very important in the life-cycle of *Z. palustris* (ssp. *repens* and ssp. *palustris*) and *Z. pedunculata*. Although these species are in fact perennials, they often occur under such environmental conditions (drought, ice-cover) that they can only survive by means of seeds. *Z. major*, however, is a perennial with a low seed production and is confined to permanent waters. The differences in community composition between the Baltic waters and the rest of the coastal zone in western Europe are clearly caused by the fluctuating chlorinity of the small habitats in more southern latitudes. The number of different habitat types within the brackish-water habitat are considered to be very important as they create habitat types with special characteristics which are inhabited by different and characteristic species combinations. Some of the chlorinity regimes in The Netherlands cause rather poor macrophyte communities. The vegetation patterns become coarser under such dynamic environmental conditions.

It is striking that the communities with *Z. pedunculata* in The Netherlands and France (Camargue) show a faunal composition more characteristic of freshwater communities than of brackish-water communities. In fact, only *Zannichellia*-dominated communities in the Baltic are true brackish-water communities according to their faunal composition. Because the structure of these communities is similar to that of the *Ruppia*-dominated communities, the freshwater character of the *Zannichellia*-dominated communities seems to be caused exclusively by the special chlorinity regimes, the drying of the habitats and the salt-tolerance of the freshwater animals.

The diversity of the *Zannichellia*-dominated communities in brackish-water expressed as H' (for numbers and biomass) is of the same order of magnitude as in freshwater communities. The number of specimens is, however, clearly larger. This is a common characteristic of brackish waters. A difference from

true brackish-water communities, however, is found in the H'_b indices. The distribution of the biomass over the different species is more like that in freshwater communities than in brackish *Ruppia*-dominated communities. The reason for this has to be looked for in the population dynamics of the characteristic species of these communities. In general it can be stated that the *Z. major*-dominated communities are true brackish-water communities. The same applies to the *Z. palustris* ssp. *repens* communities in the Baltic area although a clear, larger influence of freshwater animals is observed because this taxon often occurs in very shallow habitats near the edge of the water.

The communities with *Z. pedunculata* in The Netherlands and France are freshwater communities according to their faunal composition. Quantitatively they stand between true brackish-water and freshwater communities.

Zannichellia taxa act as a rather neutral substrate for the animals inhabiting the vegetation stands. No clear relationships were observed between the number of animals inhabiting the stands and the biomass of the aquatic macrophytes. It is very likely that there is a certain minimum biomass required to guarantee some essential demands of the fauna. The identity of the macrophytes, however, seems rather unimportant. In this respect the similarly structured *Ruppia* and *Zannichellia*-dominated communities are very similar too.

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THE ECOLOGY OF COMMUNITIES DOMINATED BY *ZANNICHELLIA* TAXA IN WESTERN EUROPE. III. CHEMICAL ECOLOGY.

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ABSTRACT

Van Vierssen, W. The ecology of communities dominated by *Zannichellia* taxa in western Europe. III. Chemical ecology.

From a number of habitats in the Netherlands where the macrophyte flora was dominated by *Zannichellia pedunculata* Rchb. the chemical constitution of the plants (Na, Ca, Mn, Mg, K, Fe, N, P) and the environment (Na, Ca, Mn, Mg, K, Fe, N, P, SO_4 and Cl) were studied. Under controlled conditions, the element content of *Z. pedunculata* was studied in relation to the element content of a sediment gradient and the chlorinity of the water. The chlorinity of the water (and the related K/Ca, K/Mg and Ca/Mg ratios) clearly affected the K/Ca, K/Mg and Ca/Mg ratios in the plants but the different sediments did not. In the field there are generally large differences in the element content between the plant parts above- and belowground. For *Z. pedunculata* mathematical equations for the relationships between the element content in these plant parts are given. When comparing *Z. pedunculata*, *Potamogeton pectinatus* L. and *Potamogeton pusillus* L. on the basis of their element content, the potassium content was different in these macrophytes. From a cluster analysis with the complete set of elements per plant part, the parts of one species appeared to cluster. The cluster with the plant parts of *Z. pedunculata* was clearly characterized by the potassium content.

The K/Mg, K/Ca and Ca/Mg ratios in *Z. pedunculata* collected in the field clearly characterize this species when compared with species such as *Potamogeton pusillus* and *Ruppia* taxa from neighbouring habitats.

When analysing the total amount of an element stored in several parts of the ecosystem such as the water layer, the sediments, the seston and the aquatic macrophytes, it is obvious that large amounts of nitrogen are present in the macrophytes (up to 50%). The seston also stores a relevant quantity of this element (maximum 6%). The sediments are loaded with phosphorus, whereas in the aquatic macrophytes only small quantities of this element are found (10%).

INTRODUCTION

This study deals with the chemical ecology of communities dominated by *Zannichellia* taxa in western Europe (see also Van Vierssen, 1982a, 1982c). The aim of this part is to describe the element constitution of a number of

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ecosystem compartments such as the water, the sediment, the seston and the aquatic macrophytes and to find out whether there are large differences in nutrient storage between different aquatic macrophytes or not. The final goal is the characterization of the *Zannichellia*-dominated communities in brackish waters according to the distribution of a number of selected elements (N, P, K, Na, Ca, Mg, Mn, Fe) over the different aquatic macrophytes in relation to the chemical characteristics of the habitat. To reach this goal these types of ecosystems were analyzed as follows.

Part of this study was restricted to a selected number of brackish waters on the island of Terschelling (the Netherlands). It was expected that the differences between the chemical characteristics of the aquatic macrophytes (and the community types) would be more obvious in a small area with similar general habitat characteristics and different community types than when they occur in communities located in a relatively wide area with very different habitat types.

Many distribution patterns of aquatic macrophytes in the brackish communities with *Z pedunculata* can be explained by e.g. their chlorinity tolerance or their drought-resistance. However, differences in occurrence and abundance which cannot be explained by such factors also exist.
This part of the study deals partly with such differences that are possibly caused by a selected uptake of elements resulting in a differentiation between species with respect to their element constitution.

To characterize the sampling stations chemically, the element concentrations in the water (Na, K, Ca, Mg, Mn, Fe, P-PO_4, NH_4, NO_3/NO_2, Cl, SO_4) and in the sediments (Na, K, Ca, Mg, Mn, Fe, N_{tot}, P_{tot}) were determined. The element constitution of the aquatic macrophytes was also determined (Na, K, Ca, Mg, Mn, Fe, N_{tot}, P_{tot}) and these were compared with a number of freshwater macrophytes from other localities as a reference. Then a study was made to find out whether there are obvious relationships between the element constitution of the plants and that of the environment or not. The different macrophyte species were compared by means of a cluster analysis. Finally the significance of the chemical characteristics of *Z pedunculata* for the entire ecosystem in which this plant grows is determined.

CHEMICAL CHARACTERIZATION OF THE SAMPLING STATIONS

Material and methods

As was pointed out in the introduction, aquatic macrophytes were collected in a large number of habitats which for the largest part belong to the A7-A9 community type (see Van Vierssen, 1982c). To compare the element constitution of the aquatic macrophytes with that of the environment, two ecosystem compartments were sampled viz, the ambient

water and the sediments. Throughout 1978 once a month water samples were collected in polyethylene bottles (250 ml), filtered (3μm), preserved (200 ppm $HgCl_2$ solution) and stored at -10°C. The Na, K, Mg, Mn, Ca, Cl, NO_3 /NO_2, NH_4 and P-PO_4, Fe, SO_4 concentrations were determined by means of flame-spectrophotometrical and spectrophotometrical methods. The chemical characteristics of the most important sampling station types were illustrated by means of Maucha-diagrams (Maucha, 1932)

In most cases, 5 sediment samples were collected from the top 5 cm layer (35 ml each) and mixed. After this material had been dried (24h, 105°C) an amount, 50 g dry weight, was chemically digested according to Kotz et al. (1972) and Verhoeven (1979). By means of cluster analysis (Clustan, D Wishart 1975) a classification of the sampling stations on the basis of a complete set of either the sediment characteristics or the characteristics of the water (i.e. the different element concentrations) was made according to two methods (Ward, Group Average). In fact, samples from one station collected at different times are considered to be separate cluster-objects. As a coefficient of dissimilarity the squared Euclidian distance with respect to standardized values for each ion or element concentration has been used. The Group Average method resulted in approximately the same clusters as the Ward method. Therefore, only the results of the Ward method are presented here.

The elements which cause the coherence of a cluster were determined by means of their F-ratios i.e. the variances of the standardized scores, while the separation between clusters was assessed by t-values, i.e. the mean of the standardized scores.

For the classification of the chemical elements, the Group Average method was applied For this analysis only samples with a complete set of concentrations have been considered As a coefficient of similarity, 1/2 + 1/2r was used, where r indicates the Pearson correlation. In order to assess as correctly as possible the chemical elements with highly negative correlations a change of sign has been applied with respect to a small number of elements

Characterization of the water

Table I gives the results of the water analyses of a number of sampling stations representative for all stations from which aquatic macrophytes were sampled (see table II) The results are means calculated from the monthly samples. The cluster analysis based on 11 ion or element concentrations leads to a general division into two clusters. After each fusion step a relocation procedure was carried out. Having obtained 6 clusters it appeared that only a few samples moved after the creation of two clusters In fig. 1 the community types which dominate one cluster are indicated in the relevant boxes. The A6 community type is clearly dissimilar to the rest of the community types. It consists of *Ruppia maritima* var. *maritima*, *Z pedunculata*, *Potamogeton pectinatus* and *Enteromorpha* spec. The sodium

Element:	Station:	N:	Mean:	S.D.:
N_{tot} (μmol/l)	1	9	134	41
	2	9	201	101
	6	9	144	58
	7	9	147	68
	15	12	83	24
	19	3	67	18
	21	1	25	—
	22	1	25	—
Na (10 μmol/l)	1	9	23	4
	2	9	137	42
	6	9	423	370
	7	9	87	36
	15	12	937	658
	19	3	11	3
	21	1	3	—
	22	1	4	—
Fe (0.1 μmol/l)	1	9	12	12
	2	9	57	62
	6	9	17	21
	7	9	19	14
	15	12	7	4
	19	3	9	4
	21	1	3	—
	22	1	8	—
SO_4 (10 μmol/l)	1	9	24	14
	2	9	94	45
	6	9	221	128
	7	9	61	25
	15	12	642	166
	19	3	54	5
	21	1	25	—
	22	1	51	—

Element:	Station:	N:	Mean:	S.D.:
P-PO_4 (μmol/l)	1	9	54	28
	2	9	84	38
	6	9	51	36
	7	9	41	16
	15	12	52	40
	19	3	6	3
	21	1	1	—
	22	1	2	—
Mg (10 μmol/l)	1	9	72	12
	2	9	235	77
	6	9	407	204
	7	9	185	66
	15	12	1079	584
	19	3	35	7
	21	1	27	—
	22	1	99	—
Ca (10 μmol/l)	1	9	127	25
	2	9	103	25
	6	9	150	45
	7	9	100	22
	15	12	227	104
	19	3	118	13
	21	1	52	—
	22	1	52	—

Element:	Station:	N:	Mean:	S.D.:
K (10 μmol/l)	1	9	41	8
	2	9	68	15
	6	9	95	34
	7	9	57	15
	15	12	231	85
	19	3	10	1
	21	1	3	—
	22	1	8	—
Mn (0.1 μmol/l)	1	9	6	5
	2	9	25	42
	6	9	18	20
	7	9	9	10
	15	12	112	308
	19	3	16	7
	21	1	3	—
	22	1	5	—
Cl (100 μmol/l)	1	9	25	3
	2	9	134	54
	6	9	313	174
	7	9	87	31
	15	12	932	423
	19	1	11	—
	21	1	11	—
	22	1	5	—

TABLE I:
General survey of the variation in element and ion concentration in the water samples. 1. Ditch Terschelling (freshwater); 2. Ditch Terschelling (A7 community type); 6. Ditch Terschelling (A7 community type); 7. Ditch Terschelling (A7 community type); 15. Polder reservoir, Zeeuws-Vlaanderen (A6 community type); 19. Former river bed, Lith (B2 community type); 21. Untersee, Lake Constance (W. Germany, B2 community type); 22. Mühlbach (W. Germany, C2 community type).

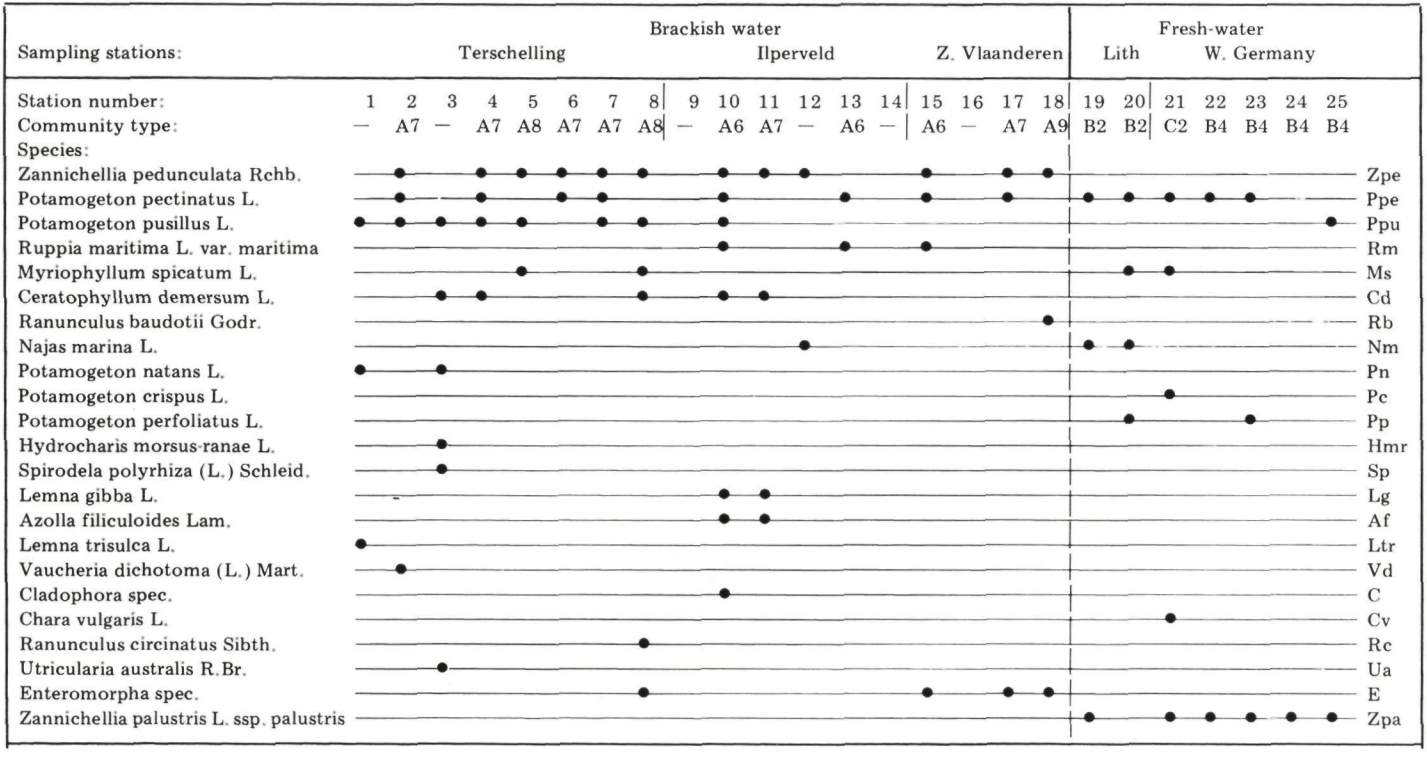

TABLE II:
Survey of the sampling stations with their aquatic macrophytes.

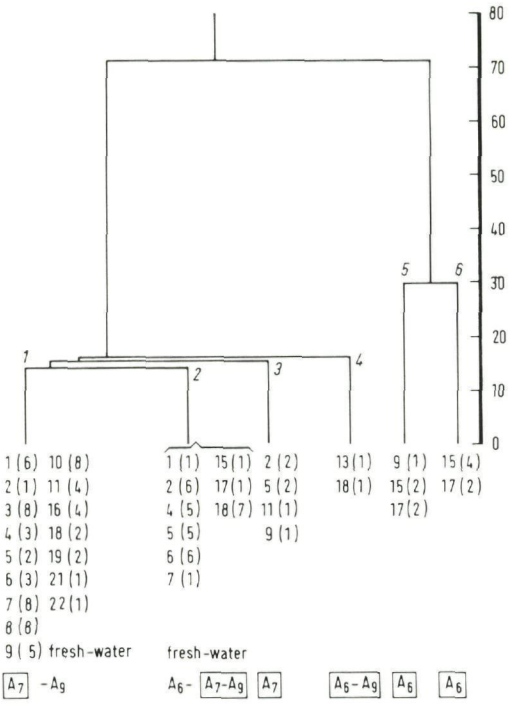

Fig. 1: Dendrogram resulting from a hierarchic fusion procedure of Ward for 113 water-samples from different sampling stations on the basis of a complete set of elements. For sampling station codes see table II. The number in brackets gives the number of watersamples from each sampling station in one cluster collected throughout the growing season. The figures along the vertical axis indicate the level of clustering.

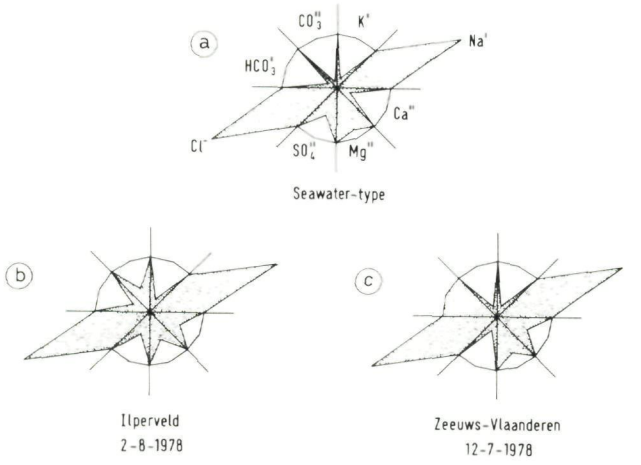

Fig. 2: Maucha diagram of a number of water types.
A. Maucha diagram of seawater.
B. Maucha diagram of a sampling station in the Ilperveld with dominant stands of *Zannichellia pedunculata* Rchb. (A7 community type).
C. Maucha diagram of a sampling station in Zeeuws-Vlaanderen with dominant stands of *Z. pedunculata* (A9 community type).

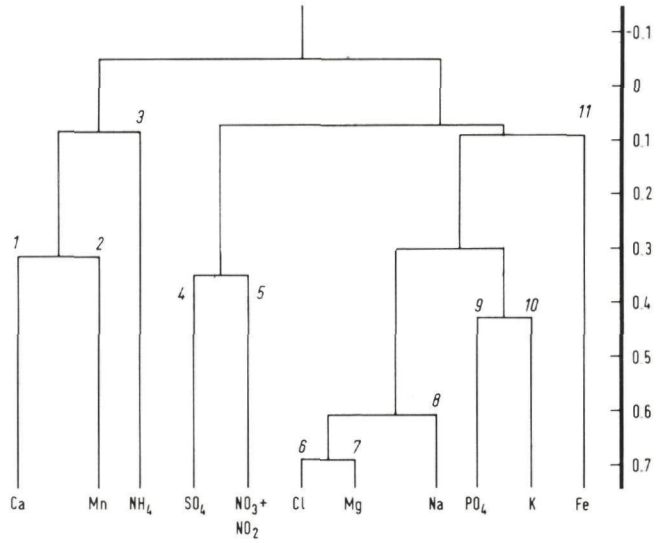

Fig. 3: Dendrogram resulting from a hierarchic Group Average fusion procedure for 11 chemical elements based on 73 watersamples from sampling stations with dominant stands of *Z. pedunculata*. The number along the vertical axis indicates the level of clustering being the average Pearson correlation for pairs of elements, one from each cluster. A change of sign has been applied for the SO_4, NO_3/NO_2 and Fe concentrations.

and chloride concentrations are responsible for this dissimilarity. Within the cluster consisting of cluster 5 and 6 the coherence is largely determined by the iron and manganese concentrations. Within the large cluster (1, 2, 3, 4) this coherence is achieved in the first place by the relatively low sodium, chloride and magnesium concentrations.

Fig. 2 gives the two types of Maucha diagrams for the community types representative for the most important clusters. As a reference, the Maucha diagram of seawater is also given. Large similarities are obvious.

In fig. 3 the results of the cluster analysis of the element concentrations in the water samples of the sampling stations 2, 4-7, 9-14, 18 are given (community types A6-A7-A8-A9). It is obvious that the magnesium, chloride and sodium concentrations show high correlations.

Characterization of the sediments

Apart from the water layer, it is obvious that the sediments are a source of nutrients for the aquatic macrophytes. By means of the methods mentioned on p. 165 a cluster analysis was carried out with the element concentrations in the sediments from a representative group of sampling stations.

After the initial analysis, a second analysis was carried out starting with 5 clusters (Ward method) and a relocation after each fusion. Almost the same results were obtained, because only a few samples moved from one cluster to another one.

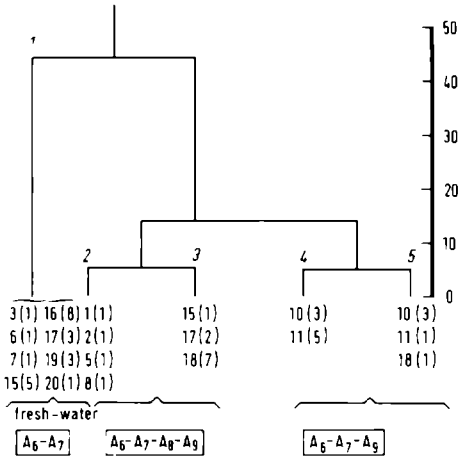

Fig. 4: Dendrogram resulting from the hierarchic fusion procedure of Ward for the element constitution of the sediments of 50 samples from different sampling stations based on a complete set of elements. For sampling station codes see table II. The numbers in brackets give the number of sediment samples in one cluster collected throughout the growing season in one sampling station. The figures along the vertical axis indicate the level of clustering.

In fig. 4 the dendrogram with the results of the analysis without relocation is given. It is obvious that using sediment constitution the clustering of the sampling stations clearly differs from the clustering using the water analyses. It turns out that according to the F-ratios and the t-values cluster 1 is characterized by a coherence which is in the first place determined by a low nitrogen and phosphorus content of the sediments. In the clusters formed by the smaller clusters 2, 3 and 4, 5 there are no characteristic elements.

Discussion and conclusions

From the results it follows that the environment of the brackish communities which were studied is characterized by an element composition resembling that of seawater. This was clearly demonstrated by the cluster analysis and the Maucha diagrams. Both A6 and the less brackish A7-A9 communities are characterized by their specific sodium and chloride concentrations. The grouping of the sampling stations according to the sediment constitution shows that only the sampling stations on Terschelling and in Zeeuws-Vlaanderen have similar specific characteristics, viz. they all have a low nitrogen and phosphorus content.

Material and methods

In order to evaluate the importance of the nutrient levels in the sediments to *Z. pedunculata*, the nutrient levels in this species were studied in relation to different substrates and chlorinities under controlled conditions.

In fact the *Z. pedunculata* plants which were cultured under controlled conditions in the "substrate preference" and chlorinity tolerance experiments (Van Vierssen, 1982a) were digested as described on p. 165.

TABLE III:
Comparisons of the element content of *Z. pedunculata* plant parts grown at the highest clay content (or the highest chlorinity) with the content of plants grown at the lowest clay content (or chlorinity). The highest clay content is given as 100 (sediments with 32.6% particles $< 2\mu m$), the lowest as 0 (1% of particles $< 2\mu m$). The sediments with 25, 50 and 75% clay are mixtures of these sediments. The highest chlorinity is given as 100 also (= 7.24‰ Cl') and the lowest as 0 (freshwater). In column A III, the percentage of clay at which the plant parts contained the highest element content (M) are given. In column B II these maxima are given for the four chlorinities used in the cultures, ranging from freshwater (1) up to 7.24‰ Cl' (4) (for exact data see fig. 5A).

A. Sediments						B. Chlorinity			
Element	I	II		III		I		II	
	Clay	Plant: Above-ground	Below-ground	Tendency Plant: Above-ground	Below-ground	Plant: Above-ground	Below-ground	Tendency Plant: Above-ground	Below-ground
	100:0	100:0	100:0			100:0	100:0		
Na	5.3	1.85	*	M75	*	1.48	3.25	M2	M4
K	27.0	1.35	*	M25	*	0.57	0.52	M1	M1
Mg	52.0	1.06	*	—	*	1.23	1.20	M2	M2
Ca	76.0	1.00	*	M75	*	0.57	0.49	M2	M1
Fe	10.0	6.60	*	M25	*	1.15	0.84	M2	M1
Mn	7.0	1.00	*	—	*	2.13	1.43	M4	M3
N_{tot}	12.2	1.26	*	M50	*	0.64	0.88	M1	—
P_{tot}	4.25	2.18	*	M25	*	1.26	1.11	—	—

Results

The results are summarized in table III. Column I gives the ratios of the concentrations of an element in a sediment with the highest clay content (indicated as 100)$^+$ and with the lowest clay content (indicated as 0)$^+$. The

same ratios were determined for the *Zannichellia* plants (i.e. for the above- and belowground plant parts respectively) grown on these different substrates (see column II). Ratios could not be calculated for the plants grown on sand as there was insufficient production of belowground plant parts for digestion, and they are thus indicated by *. Column III indicates the clay content (0, 25, 50, 75, 100 per cent clay) at which the nutrient content (indicated with letter M) of the plant parts was highest.

A similar procedure was followed for the plants grown under different chlorinities (100=7.24‰ Cl' and 0 is freshwater). The nutrient contents of the sediments were highest in those with the highest clay content. This is not reflected by the nutrient concentrations in *Z. pedunculata.* Some elements have their maximum at low clay contents (potassium, iron, phosphorus), others at relatively high clay contents (sodium and calcium) and some are not affected by the element constitution of the substrate (magnesium and manganese). From table IIIB it follows that the maximum element contents are mostly found at the lower chlorinities (the same substrate was used in all experiments).

A study was also made to establish whether any relationships existed between certain element ratios in the *Zannichellia* plants and the sediment constitution or the chlorinity of the water. The Ca/Mg, K/Mg and the K/Ca ratios in the *Zannichellia* plants were calculated from the results of the same experiment. The results are given in fig. 5 (A, B), 6 (A, B) and 7 (A, B) respectively. The shaded area in the chlorinity figures gives the range of the ratios as found for the plants cultured on different substrates (the figures B). The different sediment characteristics do not seem to have the same influence on the element ratios in the plants that the different chlorinities have. The Ca/Mg in particular and the K/Mg ratio to a lesser extent diminish with rising chlorinities.

Discussion and conclusions

The culture experiments did not reveal any obvious relationships between the element content of the plants and that of the sediments. According to the criteria of Gerloff & Krombholz (1966) a deficiency of nitrogen and phosphorus is unlikely to be responsible for the retarded growth on the sandy substrates. It is important to realize that the difference in sediment constitution in the culture experiments are relatively large. In the field these differences were often negligible. The results of the chlorinity experiment

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+ The figures 100 and 0 indicate the two substrate types which were used to make the different sediment characteristics, partly by mixing different amounts of these types. These two substrates comprised 32.6% and 1% particles of less than 2 μm respectively. The 100 figure indicates a silty loam clay, abbreviated as clay in the figures 5-7 and the following text. The 0 figure indicates sand and the 25, 50 and 75 figures, mixtures of the sand and clay material.

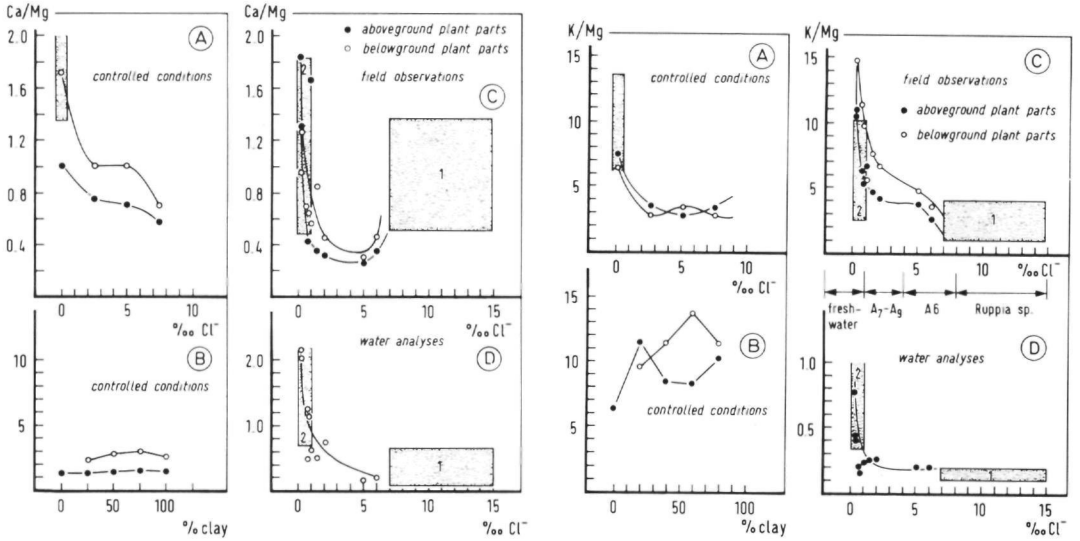


Fig. 5: Relationships between the molar Ca/Mg ratio in *Z. pedunculata*, the sediments and the water.

A. Relationship between the molar Ca/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) and the chlorinity of the water under controlled conditions.
B. Relationship between the molar Ca/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) and the sediment constitution under controlled conditions (100=32.6% sediment particles $< 2\mu$m).
C. Relationship between the molar Ca/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) in relation to the chlorinity of the water in the field. The areas 1 and 2 indicate the figures found in *Ruppia* and *Potamogeton pusillus* respectively.
D. Relationship between the molar Ca/Mg ratio in the water samples from habitats with *Z. pedunculata* (Terschelling) and the chlorinity. The areas 1 and 2 indicate the Ca/Mg ratios as found in the sampling stations with *Ruppia* and *Potamogeton pusillus* respectively.

Fig. 6: Relationship between the molar K/Mg ratio in *Z. pedunculata*, the sediments and the water.

A. Relationship between the molar K/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) and the chlorinity of the water under controlled conditions.
B. Relationship between the molar K/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) and the sediment constitution under controlled conditions (100=32.6% sediment particles $< 2\mu$m).
C. Relationship between the molar K/Mg ratio in *Z. pedunculata* (aboveground and belowground parts) in relation to the chlorinity of the water in the field. The areas 1 and 2 indicate the figures found in *Ruppia* and *Potamogeton pusillus* respectively. In this figure the chlorinity tolerance limits of different community types with different aquatic macrophytes are given. The A7-A9, A6 communities were distinguished by Van Vierssen (1982a) and refer to communities dominated by *Z. pedunculata*.
D. Relationship between the molar K/Mg ratio in the watersamples from the habitats with *Z. pedunculata* (Terschelling) and the chlorinity. The areas 1 and 2 indicate the K/Mg ratios as found in the sampling stations with *Ruppia* and *Potamogeton pusillus* respectively.

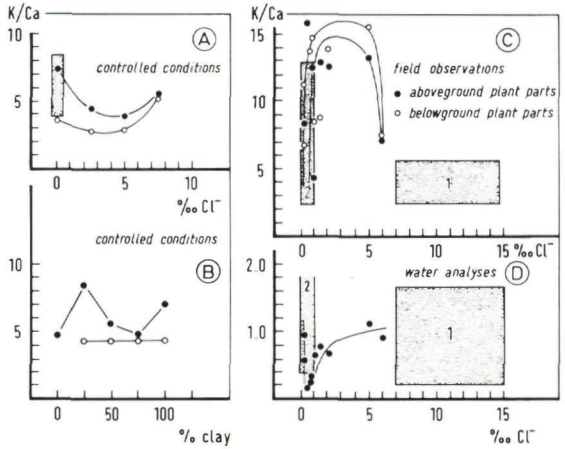


Fig. 7: Relationship between the molar K/Ca ratio in *Z. pedunculata*, the sediments and the water.

A. Relationship between the molar K/Ca ratio in *Z. pedunculata* (aboveground and belowground parts) and the chlorinity of the water under controlled conditions.

B. Relationship between the molar K/Ca ratio in *Z. pedunculata* (aboveground and belowground parts) and the sediment constitution under controlled conditions (100=32.6% sediment particles $< 2\mu m$).

C. Relationship between the molar K/Ca ratio in *Z. pedunculata* (aboveground and belowground parts) in relation to the chlorinity of the water in the field. The areas 1 and 2 indicate the figures found in *Ruppia* and *Potamogeton pusillus* respectively.

D. Relationship between the molar K/Ca ratio in the water samples from habitats with *Z. pedunculata* (Terschelling) and the chlorinity. The areas 1 and 2 indicate the K/Ca ratios as found in the sampling stations with *Ruppia* and *Potamogeton pusillus* respectively.

are therefore more important for a comparison of field data with experimental data.

It seems obvious that an increasing chlorinity generally results in decreasing Ca/Mg and K/Mg ratios. This is caused by the relatively low Ca and K concentrations in *Z. pedunculata* at relatively high chlorinities. It is important to state that in the chlorinity experiment the three ratios in the water were approximately the same at all chlorinities because the chlorinities were obtained by diluting seawater with water relatively poor in potassium, calcium and magnesium.

ELEMENT CONSTITUTION OF AQUATIC MACROPHYTES IN THE FIELD

Material and methods

In this section the differences in element composition between different parts of the macrophytes mentioned below are discussed. Further, the

relationships between the element content of these different plant parts are mathematically described.

From a selected number of the most important macrophytes in the brackish communities with *Z. pedunculata*, viz. *Z. pedunculata*, *Potamogeton pectinatus* and *Potamogeton pusillus*, the differences in element content between the aboveground and belowground plant parts have been studied with respect to three types of data.

Using t-statistics the hypothesis that the average of the theoretical differences between the element content of the plant parts from the different sampling stations was zero was tested. In the first place the real differences between the element content of the aboveground and belowground plant parts were used. Secondly the percentual differences were used in two different ways, viz. the difference between the element content of the aboveground and belowground plant parts as percentage of the element content of the aboveground plant parts and as percentage of the element content of the belowground plant parts. It can be stated that with respect to the latter test results (p-values) most attention has been paid to the results obtained when these differences were expressed as percentages of the highest element content (either in the aboveground or in the belowground plant parts).

Mathematical descriptions of the relationships between the element content in the aboveground and the belowground parts were carried out by means of a multiple linear regression and a simple linear regression analysis. The aboveground element content was considered as the independent variable and the belowground element content as the dependent variable. Whether this dependence could be described better by a second or third degree polynomial than by a simple linear relationship was then considered. Before examining these relationships however, a one-way analysis of variance was carried out together with a multiple comparison according to Scheffé to exclude aberrant samples. This analysis was done separately for each of the three plant species both for the aboveground and the belowground plant parts.

In addition to this analysis, the differences between *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* were considered on the basis of a simultaneous study of the element content of both the aboveground and the belowground plant parts of plants growing together. Only two plants were compared simultaneously. In the first place it was necessary to establish that no obvious differences existed between the covariance matrices of both variables (element content of the aboveground and belowground plant parts) for the two macrophytes being compared. This was achieved by a generalization of the Bartlett test. After this preliminary test, the multivariate Hotelling-T^2 test for two samples was carried out to examine the differences between two taxa. Simultaneous confidence intervals for the means of the element content of the aboveground and belowground plant parts were used to explain significant test results. Only data of macrophytes growing together were used for the comparison of two plants.

TABLE IV
Element contents of aquatic macrophytes expressed as % of plant dry weight.
A = Aboveground, B = Belowground.

Element: K (%)							Element: Na (%)				
Species:		Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min
Zannichellia pedunculata	A	4.84	1.42	46	10.00	1.98	1.42	0.99	45	4.39	0.46
	B	6.02	1.14	43	7.77	3.91	1.70	0.86	40	4.41	0.67
Potamogeton pectinatus	A	3.51	0.84	21	5.34	1.61	1.68	1.10	19	4.00	0.55
	B	4.11	1.29	17	6.78	2.52	1.10	0.79	16	3.77	0.39
Potamogeton pusillus	A	2.73	0.76	15	4.89	1.83	0.91	0.29	15	1.33	0.51
	B	3.72	1.04	13	5.28	1.72	0.93	0.39	13	1.98	0.51
Myriophyllum spicatum	A	2.23	0.49	5	2.96	1.69	1.41	0.41	5	1.93	0.80
	B	3.10	0.74	4	3.90	2.11	1.02	0.20	4	1.26	0.85
Ruppia maritima var. maritima	A	4.34	0.53	6	4.59	3.73	1.79	1.44	5	3.38	0.60
	B	5.68	0.55	4	6.05	4.87	1.65	1.37	3	3.22	0.71
Ranunculus baudotii	A	6.27	3.22	2	8.54	3.99	1.39	0.21	2	1.54	1.24
	B	4.56	1.22	2	5.42	3.69	1.16	0.18	2	1.29	1.03
Najas marina	A	7.23	2.02	3	9.34	5.32	1.94	0.06	2	1.98	1.94
	B	6.36	1.37	2	7.33	5.39	3.21	1.59	2	4.32	2.09
Zannichellia palustris	A	4.72	0.88	6	5.85	3.40	1.35	0.57	6	2.05	0.78
	B	4.69	0.72	5	5.96	4.22	1.66	0.37	5	2.05	1.29
Potamogeton natans,											
floating leaves:		2.78	0.30	4	2.97	2.33	0.80	0.17	4	0.97	0.60
stems:		4.25	1.90	4	7.01	2.85	0.66	0.33	4	1.15	0.46
belowground:		3.11	0.94	2	3.78	2.45	0.14	0.00	2	0.14	0.14
Potamogeton crispus											
leaves:		2.11	—	1	—	—	0.87	—	1	—	—
stems:		5.41	—	1	—	—	0.67	—	1	—	—
Potamogeton perfoliatus											
leaves:		1.56	—	1	—	—	0.85	—	1	—	—
stems:		6.30	—	1	—	—	0.90	—	1	—	—
belowground:		4.80	—	1	—	—	1.03	—	1	—	—
Hydrocharis morsus-ranae											
leaves:		4.07	—	1	—	—	1.75	—	1	—	—
stems:		5.81	—	1	—	—	2.34	—	1	—	—
Enteromorpha spec.		1.58	0.33	7	1.81	0.87	0.75	0.64	7	1.98	0.18
Ceratophyllum demersum		4.89	1.24	8	7.01	3.21	0.61	0.15	8	0.83	0.41
Azolla filiculoides		3.01	0.35	3	3.40	2.72	1.67	0.17	3	1.86	1.54
Utricularia australis		3.79	0.12	2	3.87	3.70	1.49	0.18	2	1.61	1.36
Vaucheria dichotoma		0.86	—	1	—	—	0.62	—	1	—	—
Chara vulgaris		1.07	0.49	7	1.85	0.63	0.37	0.11	7	0.57	0.23
Lemna trisulca		4.11	—	1	—	—	1.31	—	1	—	—
Lemna gibba		3.60	0.64	5	4.64	3.14	1.02	0.20	5	1.31	0.78
Spirodela polyrhiza		4.17	0.44	2	4.48	3.86	0.74	0.06	2	0.78	0.69
Cladophora spec.		1.54	1.49	4	3.57	0.35	1.51	1.65	4	3.54	0.14
Ranunculus circinatus	A	4.40	—	1	—	—	1.13	—	1	—	—
	B	5.94	—	1	—	—	1.47	—	1	—	—

TABLE IV: (continued)

Element: Fe (%)							Element: Mn (%)				
Species:		Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min
Zannichellia pedunculata	A	0.15	0.20	48	1.22	0.02	0.12	0.09	48	0.54	0.03
	B	0.29	0.31	44	1.72	0.04	0.17	0.16	44	0.83	0.04
Potamogeton pectinatus	A	0.10	0.07	21	0.33	0.03	0.14	0.17	21	0.53	0.01
	B	0.32	0.52	17	2.25	0.07	0.04	0.04	17	0.13	0.01
Potamogeton pusillus	A	0.14	0.08	15	0.28	0.04	0.16	0.14	15	0.46	0.04
	B	0.96	1.29	13	4.86	0.22	0.11	0.08	13	0.33	0.01
Myriophyllum spicatum	A	0.10	0.04	5	0.14	0.05	0.30	0.26	5	0.67	0.04
	B	0.80	0.92	4	2.15	0.05	0.18	0.12	4	0.33	0.05
Ruppia maritima var. maritima	A	0.11	0.09	6	0.28	0.04	0.34	0.24	6	0.62	0.07
	B	0.18	0.09	4	0.26	0.08	0.44	0.57	4	1.30	0.13
Ranunculus baudotii	A	0.09	0.02	2	0.10	0.08	0.09	0.02	2	0.10	0.07
	B	0.46	0.37	2	0.73	0.20	0.22	0.04	2	0.25	0.20
Najas marina	A	0.39	0.42	3	0.87	0.09	0.20	0.23	3	0.46	0.01
	B	0.24	0.15	2	0.35	0.13	0.11	0.05	2	0.14	0.07
Zannichellia palustris	A	0.18	0.25	6	0.69	0.04	0.03	0.02	6	0.06	0.01
	B	0.22	0.13	5	0.45	0.14	0.03	0.05	5	0.12	0.01
Potamogeton natans											
floating leaves:		0.10	0.07	4	0.21	0.06	0.05	0.04	4	0.08	0.02
stems:		0.10	0.07	4	0.19	0.03	0.10	0.10	4	0.19	0.01
belowground:		0.27	0.23	2	0.43	0.10	0.02	0.00	2	0.02	0.02
Potamogeton crispus											
leaves:		0.03	—	1	—	—	0.02	—	1	—	—
stems:		0.06	—	1	—	—	0.01	—	1	—	—
Potamogeton perfoliatus											
leaves:		0.10	—	1	—	—	0.02	—	1	—	—
stems:		0.07	—	1	—	—	0.02	—	1	—	—
belowground:		0.38	—	1	—	—	0.01	—	1	—	—
Hydrocharis morsus-ranae											
leaves:		0.06	—	1	—	—	0.06	—	1	—	—
stems:		0.23	—	1	—	—	0.35	—	1	—	—
Enteromorpha spec.		0.11	0.11	7	0.34	0.03	0.18	—	7	0.39	0.03
Ceratophyllum demersum		0.18	0.14	8	0.44	0.04	0.59	0.37	8	1.18	0.11
Azolla filiculoides		0.10	0.03	3	0.12	0.07	0.10	0.02	3	0.13	0.08
Utricularia australis		0.48	0.11	2	0.55	0.40	—	—	—	—	—
Vaucheria dichotoma		0.32	—	1	—	—	0.45	—	1	—	—
Chara vulgaris		0.11	0.09	7	0.26	0.04	0.29	0.33	7	1.00	0.07
Lemna trisulca		0.11	—	1	—	—	0.23	—	1	—	—
Lemna gibba		0.09	0.05	5	0.14	0.02	0.59	0.25	5	0.98	0.36
Spirodela polyrhiza		0.09	0.04	2	0.12	0.05	0.17	0.07	2	0.23	0.12
Cladophora spec.		0.06	0.02	4	0.09	0.04	0.22	0.44	4	0.89	0.00
Ranunculus circinatus	A	0.06	—	1	—	—	0.38	—	1	—	—
	B	0.25	—	1	—	—	0.34	—	1	—	—

TABLE IV: (continued)

Element: Ca (%)							Element: Mg (%)				
Species:		Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min
Zannichellia pedunculata	A	0.68	0.90	48	4.86	0.14	0.52	0.15	48	0.83	0.22
	B	0.63	0.41	44	2.35	0.24	0.45	0.19	44	0.89	0.16
Potamogeton pectinatus	A	0.62	0.26	21	1.20	0.16	0.72	0.27	21	1.36	0.17
	B	0.47	0.41	17	1.77	0.16	0.37	0.17	17	0.80	0.18
Potamogeton pusillus	A	0.52	0.24	15	1.29	0.26	0.52	0.14	14	0.94	0.40
	B	0.70	0.35	13	1.49	0.32	0.47	0.16	13	0.84	0.29
Myriophyllum spicatum	A	0.48	0.09	5	0.61	0.39	0.64	0.19	5	0.88	0.44
	B	0.50	0.17	4	0.73	0.33	0.47	0.18	4	0.73	0.33
Ruppia maritima var. maritima	A	0.43	0.08	6	0.52	0.28	0.79	0.21	6	1.14	0.58
	B	0.50	0.13	4	0.63	0.36	0.72	0.21	4	1.02	0.54
Ranunculus baudotii	A	1.61	0.14	2	1.71	1.51	0.84	0.20	2	0.98	0.70
	B	1.73	1.15	2	2.54	0.91	0.55	0.01	2	0.55	0.54
Najas marina	A	0.58	0.50	3	1.16	0.27	0.76	0.51	3	1.33	0.37
	B	0.45	0.01	2	0.46	0.44	0.67	0.18	2	0.79	0.54
Zannichellia palustris	A	0.74	0.44	6	1.19	0.08	0.46	0.06	6	0.52	0.35
	B	1.78	1.38	5	3.31	0.49	0.35	0.05	5	0.40	0.27
Potamogeton natans											
floating leaves:		1.28	1.97	4	4.24	0.24	0.51	0.16	4	0.72	0.36
stems:		1.42	2.03	4	4.46	0.28	0.52	0.16	4	0.75	0.36
belowground:		0.25	0.11	2	0.32	0.17	0.31	0.08	2	0.36	0.25
Potamogeton crispus											
leaves:		1.16	—	1	—	—	0.46	—	1	—	—
stems:		2.20	—	1	—	—	0.35	—	1	—	—
Potamogeton perfoliatus											
leaves:		0.52	—	1	—	—	0.78	—	1	—	—
stems:		0.55	—	1	—	—	0.49	—	1	—	—
belowground:		0.35	—	1	—	—	0.30	—	1	—	—
Hydrocharis morsus-ranae											
leaves:		0.28	—	1	—	—	1.19	—	1	—	—
stems:		0.32	—	1	—	—	0.76	—	1	—	—
Enteromorpha spec.		1.76	1.09	7	3.39	0.63	2.08	0.50	7	2.57	1.08
Ceratophyllum demersum		0.37	0.09	8	0.46	0.24	0.82	0.15	8	1.03	0.51
Azolla filiculoides		0.15	0.01	3	0.16	0.14	0.43	0.08	3	0.50	0.34
Utricularia australis		0.73	0.34	2	0.97	0.49	0.53	0.21	2	0.67	0.38
Vaucheria dichotoma		1.43	—	1	—	—	1.24	—	1	—	—
Chara vulgaris		6.99	3.57	7	9.68	0.54	0.41	0.15	7	0.70	0.31
Lemna trisulca		1.09	—	1	—	—	0.82	—	1	—	—
Lemna gibba		0.65	0.31	5	1.08	0.29	0.61	0.12	5	0.80	0.47
Spirodela polyrhiza		0.55	0.12	2	0.63	0.46	1.02	0.42	2	1.32	0.72
Cladophora spec.		1.38	1.67	4	3.87	0.24	0.81	0.32	4	1.28	0.56
Ranunculus circinatus	A	0.37	—	1	—	—	0.38	—	1	—	—
	B	0.45	—	1	—	—	0.40	—	1	—	—

TABLE IV: (continued)

Element: N (%)							Element: P (%)				
Species:		Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min
Zannichellia pedunculata	A	2.97	3.09	46	5.22	0.63	1.43	2.05	47	1.75	0.51
	B	1.51	0.51	42	3.10	0.32	0.76	0.24	44	1.49	0.28
Potamogeton pectinatus	A	2.12	0.83	20	4.12	1.24	0.63	0.22	20	1.11	0.14
	B	1.47	0.60	16	2.51	0.66	0.53	0.20	17	0.91	0.17
Potamogeton pusillus	A	2.50	0.73	15	4.13	1.34	0.80	0.18	15	1.17	0.55
	B	1.69	0.87	13	2.79	0.08	0.87	0.50	13	2.29	0.44
Myriophyllum spicatum	A	2.44	0.54	5	3.15	1.73	0.55	0.22	5	0.83	0.28
	B	1.64	0.51	4	2.23	1.08	0.45	0.30	4	0.70	0.08
Ruppia maritima var. maritima	A	2.24	0.65	6	2.94	1.21	0.74	0.19	6	1.02	0.55
	B	1.39	0.40	4	1.88	0.93	0.44	0.22	4	0.72	0.21
Ranunculus baudotii	A	1.26	0.43	2	1.56	0.95	0.89	0.06	2	0.93	0.85
	B	1.51	0.39	2	1.78	1.23	0.92	0.37	2	1.18	0.67
Najas marina	A	3.39	1.04	2	4.12	2.65	1.02	0.47	3	1.56	0.72
	B	1.56	0.75	2	2.09	1.03	0.40	0.10	2	0.48	0.33
Zannichellia palustris	A	2.23	0.22	5	2.50	1.91	0.88	0.23	5	0.96	0.61
	B	0.95	0.39	5	1.59	0.06	0.45	0.14	5	0.61	0.31
Potamogeton natans											
floating leaves:		1.92	0.39	4	2.17	1.34	0.45	0.02	4	0.47	0.43
stems:		0.75	0.35	4	1.07	0.34	0.33	0.07	4	0.40	0.26
belowground:		0.95	0.38	2	1.22	0.68	0.38	0.22	2	0.53	0.22
Potamogeton crispus											
leaves:		4.76	—	1	—	—	0.25	—	1	—	—
stems:		0.61	—	1	—	—	0.13	—	1	—	—
Potamogeton perfoliatus											
leaves:		2.86	—	1	—	—	0.63	—	1	—	—
stems:		0.86	—	1	—	—	0.56	—	1	—	—
belowground:		1.19	—	1	—	—	0.55	—	1	—	—
Hydrocharis morsus-ranae											
leaves:		4.19	—	1	—	—	0.77	—	1	—	—
stems:		0.71	—	1	—	—	1.03	—	1	—	—
Enteromorpha spec.		1.07	0.53	6	2.14	0.73	0.60	0.16	7	0.91	0.45
Ceratophyllum demersum		2.13	0.86	8	3.03	0.60	0.89	0.19	8	1.17	0.57
Azolla filiculoides		2.42	0.08	3	2.49	2.34	0.63	0.17	3	0.82	0.51
Utricularia australis		3.32	0.78	2	3.87	2.77	0.72	0.17	2	0.84	0.61
Vaucheria dichotoma		3.15	—	1	—	—	2.63	—	1	—	—
Chara vulgaris		1.03	0.31	7	1.55	0.07	0.31	0.16	7	0.62	0.14
Lemna trisulca		0.96	—	1	—	—	0.69	—	1	—	—
Lemna gibba		1.41	0.50	5	1.93	0.61	0.61	0.07	5	0.73	0.54
Spirodela polyrhiza		1.67	0.14	2	1.77	1.57	0.73	0.17	2	0.86	0.61
Cladophora spec.		1.24	0.07	4	1.78	0.99	0.43	0.27	4	0.80	0.18
Ranunculus circinatus	A	2.20	—	1	—	—	0.86	—	1	—	—
	B	2.06	—	1	—	—	0.62	—	1	—	—

TABLE V:
General survey of the statistical results concerning the study whether, averaged over the relevant sampling stations, the aboveground and belowground plant parts of *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* differ in their element content or not (p-values of t-test procedures). A = Aboveground, B = Belowground.

	Difference	Difference as % of A	Difference as % of B	Conclusion
Z. pedunculata				
N	< 0.0001	< 0.0001	< 0.0001	A > B
P	< 0.0001	< 0.0001	< 0.0001	A > B
K	< 0.0001	< 0.0001	< 0.0001	A < B
Na	0.0005	0.0003	< 0.0001	A < B
Ca	0.05	0.06	0.03	A < B
Mg	0.0004	< 0.0001	< 0.0001	A > B
Fe	0.0004	0.001	< 0.0001	A < B
Mn	0.08	> 0.10	> 0.10	—
P. pectinatus				
N	0.0002	0.0001	0.002	A > B
P	0.01	0.02	0.001	A > B
K	> 0.10	0.06	> 0.10	—
Na	0.06	0.08	0.03	—
Ca	> 0.10	> 0.10	0.01	—
Mg	0.002	0.06	0.0002	A > B
Fe	> 0.10	0.02	0.02	A < B
Mn	0.006	> 0.10	0.03	A > B
P. pusillus				
N	0.04	0.05	> 0.10	A > B
P	> 0.10	> 0.10	> 0.10	—
K	0.03	0.05	0.009	A < B
Na	> 0.10	> 0.10	> 0.10	—
Ca	0.04	> 0.10	> 0.10	A < B
Mg	> 0.10	0.02	0.005	A > B
Fe	0.07	0.07	0.0002	—
Mn	> 0.10	> 0.10	> 0.10	—

TABLE VI:
Similarities between *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* on the basis of differences in element content between aboveground and belowground plant parts. When the aboveground plant parts contained the highest element content, the element concerned as been indicated with *.

Zannichellia pedunculata-Potamogeton pectinatus: N*, P*, Mg*, Fe
Zannichellia pedunculata-Potamogeton pusillus: N*, Mg*, K
Potamogeton pectinatus-Potamogeton pusillus: N*, Mg*
Zannichellia pedunculata-Potamogeton pectinatus-Potamogeton pusillus: N*, Mg*

TABLE VII:
Regression equations which estimate the mean element of the aboveground plant part (A) (μmol/mg plant dry weight), given the content of the belowground plant part (B) of *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus*. In the last column the p-values are given resulting from testing the hypothesis that the coefficient of the highest degree term is zero.

		p:
Z. pedunculata:		
N:	$A = 1.74 + 0.04B$	> 0.10
P:	$A = -0.063 + 2.51B - 3.3B^2$	0.03
K:	$A = 0.22 + 0.65B$	< 0.001
Na:	$A = -0.11 + 1.5B - 0.91B^2$	0.03
Ca:	$A = -0.152 + 3.82B - 15.5B^2 + 20B^3$	0.001
Mg:	$A = 0.004 + 1.6B - 2.2B^2$	0.003
Fe:	$A = 0.017 + 0.06B$	> 0.10
Mn:	$A = 0.010 + 0.34B$	< 0.001
P. pectinatus:		
N:	$A = 1.31 - 1.05B + 1.05B^2$	0.04
P:	$A = -0.127 + 3.61B - 8.5B^2$	0.02
K:	$A = 0.75 + 0.14B$	> 0.10
Na:	$A = 0.27 + 0.60B$	0.03
Ca:	$A = 0.137 + 0.08B$	> 0.10
Mg:	$A = -0.148 + 5.12B - 12.4B^2$	0.05
Fe:	$A = 0.014 + 0.04B$	0.07
Mn:	$A = 0.001 + 3.06B$	0.002
P. pusillus:		
N:	$A = 0.86 + 5.34B - 6.49B^2 + 2.15B^3$	0.03
P:	$A = 0.266 - 0.001B$	> 0.10
K:	$A = 0.29 + 0.45B$	0.02
Na:	$A = -0.26 + 2.93B - 2.77B^2$	< 0.001
Ca:	$A = 0.173 - 1.03B + 3.7B^2$	0.03
Mg:	$A = 0.121 + 0.508B$	0.03
Fe:	$A = 0.026 - 0.005B$	> 0.10
Mn:	$A = 0.021 + 0.46B$	> 0.10

A cluster analysis according to Ward on the basis of a complete set of element contents transformed into standardized values has been used to classify the plants or plant parts. Samples from different stations and from the same station but collected at different times were considered to be separate cluster objects.

Constitution of different plant parts

In table IV the element contents of the aquatic macrophytes are given as percentages of dry plant matter. In table V the results of the tests to detect differences in the element content of different plant parts of *Z pedunculata*, *Potamogeton pectinatus* and *P. pusillus* are summarized. It can be concluded that for many elements the distribution over the aboveground and the belowground plant parts differs in these species. In table VI the similarities in trends with respect to the differences in element content of the aboveground and belowground plant parts have been summarized for *Z pedunculata*, *Potamogeton pectinatus* and *P pusillus*

Only nitrogen and magnesium are present in significantly larger concentrations in the aboveground plant parts in all three macrophyte species. The estimated regression equations which describe the relationships between the element concentration in the aboveground and the belowground plant parts have bee summarized in table VII. When a second or third degree expression is given, then the coefficient of the highest degree term differs significantly ($p<0.05$) from zero. If a higher degree expression does not apply (i.e. when in a model with a second or third degree equation the coefficient of the highest degree term cannot be proved to differ significantly from zero) a simple linear regression equation is given. Generally the regression coefficient of this linear equation does not differ significantly from zero ($p>0.10$).

Constitution of different taxa

Differences between plant parts

In table VIII the results of the investigation concerning the joint differences between the same plant parts of *Z pedunculata*, *Potamogeton pectinatus* and *P pusillus* are given. In order to find out which plant part is mainly the cause of the significant differences between two plants, the test results for each plant part, using a multiple comparison approach based on simultaneous confidence intervals for the two mean differences in element content, are also given.

From table VIII it follows that *Z pedunculata* and *Potamogeton pectinatus* differ in phosphorus, potassium, sodium and manganese element content, whereas *Z pedunculata* and *Potamogeton pusillus* differ in potassium content. *Potamogeton pusillus* and *Potamogeton pectinatus* obviously differ in iron content and possibly in potassium content (see text table VIII). It can be concluded that the potassium content is different in all these species.

TABLE VIII:
Differences in element content of different plant parts between *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus*. For each comparison of the aboveground (A) and belowground (B) plant parts the mean element content in each species is given (μmol/mg dry plant matter). The p-value from the comparison of the species (given under "total") results from a Hotelling T^2-test. The additional p-values from the comparison of separate plant parts are the result of multiple comparison tests based on simultaneous confidence intervals for the separate mean differences (see text).

N			P			K		
	Zpe-Ppe	p-value		Zpe-Ppe	p-value		Zpe-Ppe	p-value
A	2.08 1.30	—	A	0.30 0.26	> 0.10	A	1.32 0.96	0.01-0.05
B	1.11 0.84	—	B	0.24 0.16	0.05	B	1.48 1.02	0.05-0.10
Total:		> 0.10	Total:		0.05	Total:		0.02

Na			Ca			Mg		
	Zpe-Ppe	p-value		Zpe-Ppe	p-value		Zpe-Ppe	p-value
A	0.60 0.42	0.05-0.10	A	0.10 0.15	> 0.10	A	0.26 0.32	—
B	0.71 0.36	< 0.01	B	0.18 0.09	> 0.10	B	0.24 0.19	—
Total:		0.002	Total:		0.05	Total:		> 0.10

Fe			Mn		
	Zpe-Ppe	p-value		Zpe-Ppe	p-value
A	0.02 0.01	—	A	0.02 0.02	> 0.10
B	0.07 0.04	—	B	0.02 0.01	0.05-0.10
Total:		> 0.10	Total:		0.02

N			P			K		
	Zpe-Ppu	p-value		Zpe-Ppu	p-value		Zpe-Ppu	p-value
A	1.60 1.82	—	A	0.30 0.28	—	A	1.22 0.72	0.01-0.05
B	1.12 1.20	—	B	0.25 0.27	—	B	1.45 0.88	< 0.01
Total:		> 0.10	Total:		> 0.10	Total:		0.006

Na			Ca			Mg		
	Zpe-Ppu	p-value		Zpe-Ppu	p-value		Zpe-Ppu	p-value
A	0.47 0.47	> 0.10	A	0.09 0.12	—	A	0.24 0.21	—
B	0.59 0.40	> 0.10	B	0.14 0.14	—	B	0.21 0.20	—
Total:		0.07	Total:		> 0.10	Total:		> 0.10

Fe			Mn		
	Zpe-Ppu	p-value		Zpe-Ppu	p-value
A	0.02 0.01	> 0.10	A	0.02 0.02	> 0.10
B	0.07 0.04	> 0.10	B	0.02 0.01	> 0.10
Total:		> 0.10	Total:		0.07

N			P			K		
	Ppe-Ppu	p-value		Ppe-Ppu	p-value		Ppe-Ppu	p-value
A	1.06 1.50	0.05-0.10	A	0.32 0.29	> 0.10	A	1.04 0.60	> 0.10
B	0.65 1.21	> 0.10	B	0.18 0.35	> 0.10	B	0.78 0.79	> 0.10
Total:		0.07	Total:		0.08	Total:		0.03

Na			Ca			Mg		
	Ppe-Ppu	p-value		Ppe-Ppu	p-value		Ppe-Ppu	p-value
A	0.48 0.49	—	A	0.14 0.12	—	A	0.24 0.20	—
B	0.38 0.45	—	B	0.09 0.14	—	B	0.19 0.23	—
Total:		> 0.10	Total:		> 0.10	Total:		> 0.10

Fe			Mn		
	Ppe-Ppu	p-value		Ppe-Ppu	p-value
A	0.02 0.03	> 0.10	A	0.02 0.03	—
B	0.04 0.24	> 0.10	B	0.01 0.02	—
Total:		0.04	Total:		> 0.10

Differences between macrophytes from communities with Zannichellia *taxa*

In fig. 8 (A, B, C, D) the differences in the element constitution of the various aquatic macrophytes accompanying *Z. pedunculata* are visualized. In these figures the element content of *Z. pedunculata* has been considered as a reference. This means that the element concentrations in *Z. pedunculata* plants which were collected at different places and times are represented here as being on the same level. Thus the zero value indicates the element content of *Z. pedunculata* plants compared with the element contents in its accompanying macrophytes at the same sampling station at the same moment. The sequence in a horizontal direction represents the sampling sequence throughout the growing season. The time intervals between sampling were not equal (this sometimes occurred at the different stations simultaneously, sometimes at intervals of several weeks). To present a clear image a fixed interval is given in fig. 8.

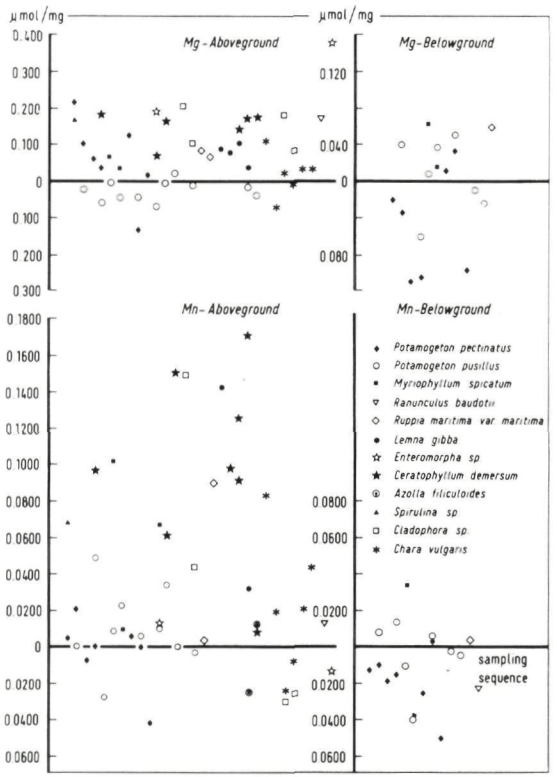
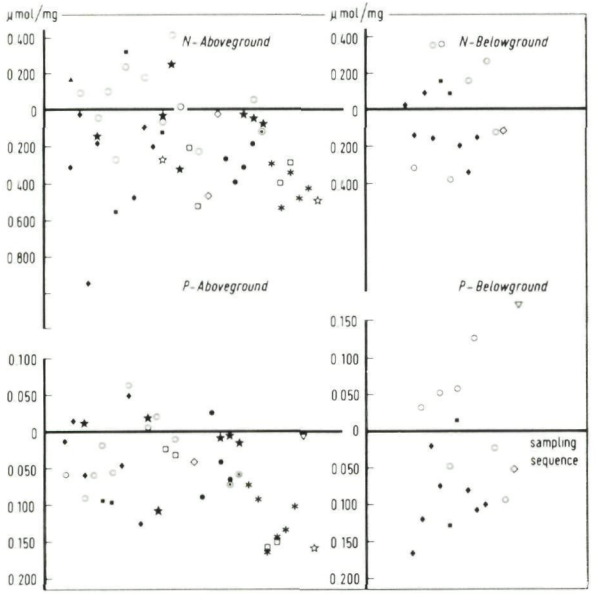
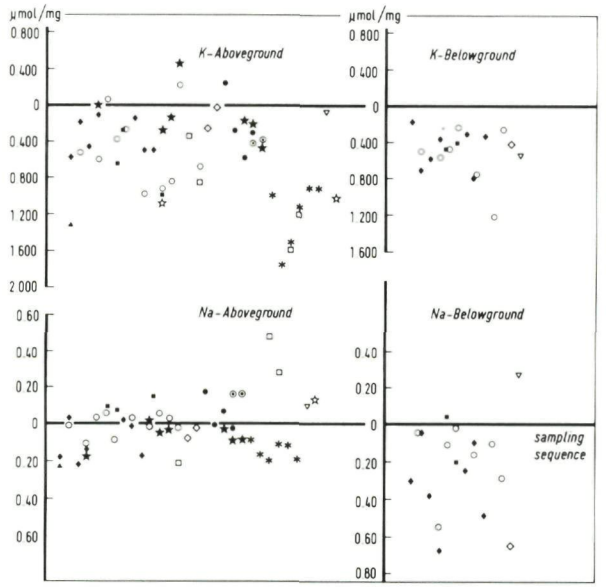


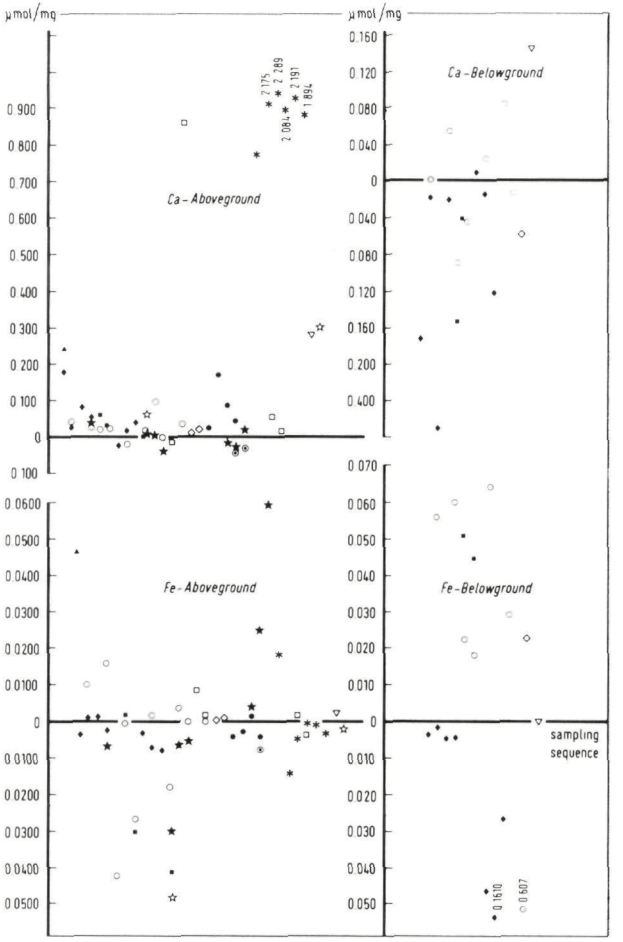
Fig. 8: Differences in element content of aquatic macrophytes growing together with *Z. pedunculata* (µmol/mg dry plant matter). The vertical axis gives the difference between the element content of *Z. pedunculata* and that of its accompanying species. The horizontal axis indicates the sampling sequence throughout the growing season. For symbols see fig. 8A.
A. Mg and Mn contents.



B. N and P contents.



C. K and Na contents.



D. Ca and Fe contents.

The magnesium concentration in the aboveground plant parts of *Z. pedunculata* is relatively low compared with the accompanying macrophytes except for *Potamogeton pusillus.* The same applies to the manganese concentrations in the plants.

It is obvious that the nitrogen content of *Z. pedunculata* is relatively high in the aboveground plant parts, but relatively low in the belowground plant parts.

The aboveground parts of *Z. pedunculata* show relatively high phosphorus contents. It is striking that the phosphorus concentration of the belowground parts of *Z. pedunculata* is obviously higher than the concentration in the belowground parts of *Potamogeton pectinatus.*

As already discussed, the potassium concentration in *Z. pedunculata* is

relatively very high and very characteristic. This element is present in relatively low quantities in *Chara vulgaris*. Sodium occurs in relatively high quantities in the belowground plant parts of *Z. pedunculata*.

The calcium concentration in (and probably partly on) *Z. pedunculata* are relatively low in the aboveground plant parts, especially compared with the concentrations in and on *Chara vulgaris*. The iron concentrations in *Z. pedunculata* plants are generally within the range of those found in the other plants.

Comparing the results of the element constitution of *Z. pedunculata* with this of the accompanying macrophytes it is obvious that *Z. pedunculata* has very characteristic nitrogen, potassium, phosphorus, magnesium and manganese concentrations in the aboveground plant parts. The potassium and sodium concentrations in the belowground plant parts are also very characteristic.

Cluster analysis with the complete set of elements

The results of a cluster analysis with the complete set of elements is given

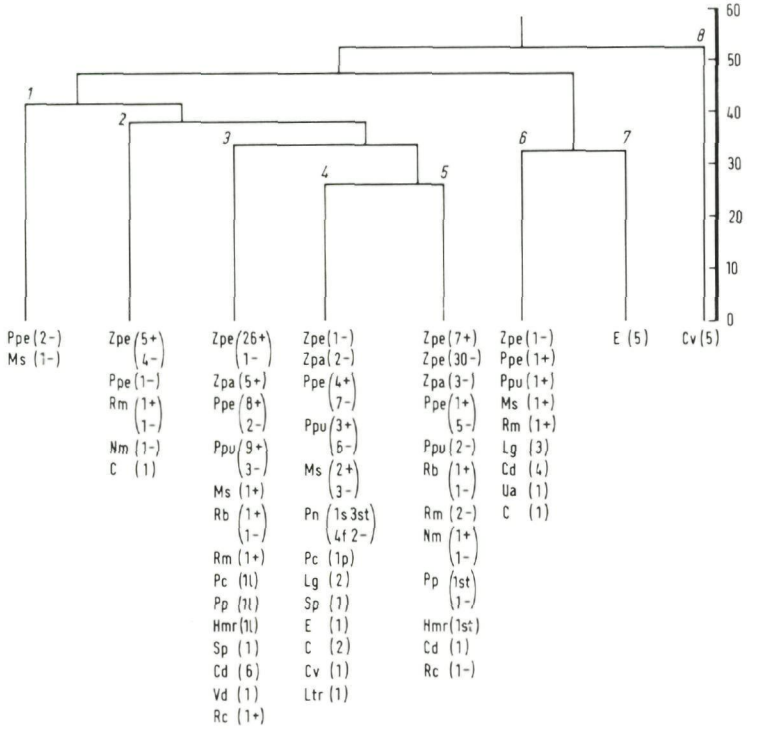


Fig. 9: Dendrogram resulting from a hierarchic fusion procedure of Ward with relocation for 219 plants or plant parts on the basis of the complete set of elements. The numbers in brackets indicate the number of samples in the cluster. The figures along the vertical axis indicate the level of clustering. + = Aboveground, − = Belowground, s = submerged leaves, f = floating leaves, st = stems, l = leaves, no abbreviation = entire plant.

in fig. 9. The eight clusters given in this figure were obtained after application of a relocation procedure. Likewise, after each following fusion step relocation was applied.

Quite a few cluster objects moved repeatedly from one cluster to another. Only the clusters 1 and 8 remained unchanged.

It is striking that in spite of the fact that the species were collected from a relatively large number of different habitats the plant parts of one species clearly cluster. The environmental heterogeneity of these different habitats does not result in a clustering of accompanying macrophytes but in a clustering of plant parts of the same species. This is clearly illustrated by *Z. pedunculata* and *Potamogeton pectinatus.* The majority of the aboveground parts of *Z. pedunculata* are found in cluster 3 whereas the majority of the belowground parts are found in cluster 5. The majority of the aboveground parts of *Potamogeton pectinatus* are found in cluster 3 (and 4), whereas the belowground parts are found in the clusters 4 and 5. The iron, potassium and magnesium contents of the *Z. pedunculata* plant parts determine the characteristics of the clusters with the majority of the parts of this species. *Enteromorpha* and *Chara vulgaris* obviously have a very characteristic element content because they form separate clusters. The *Enteromorpha* cluster is separated from all other clusters by a high magnesium content and the *Chara vulgaris* cluster by its high Ca content (or better, its calcium incrustations).

Relationships between biotic and abiotic components in the coenoses with Z. pedunculata

A study using material from a selected number of sampling stations was made to determine whether a significantly positive or negative correlation existed between element concentrations in the plant parts of *Z. pedunculata* and the element contents of the sediments or not. This examination did not give clear results.

It seems, however, that some clear relationships exist between the molar K/Mg, K/Ca and Ca/Mg ratios in the plant parts of *Z. pedunculata* and the chlorinity of the water in the sampling stations. In fig. 5C it can be seen that a clear relationship exists between the Ca/Mg ratio in the aboveground and belowground plant parts of *Z. pedunculata* plants collected in the field (Terschelling) and the chlorinity of the water. In the areas 1 and 2 the ratios as found in *Ruppia* species (area 1, data from Verhoeven, 1979) and those found in *Potamogeton pusillus* (area 2, Terschelling) are given. In fig. 5D, the same ratio has been calculated for the water in which these plants grow. The numbers 1 and 2 refer to the sampling stations in which *Ruppia* taxa and *Potamogeton pusillus* were collected. It can be seen that a similar relationship exists. It is obvious however that the more saline the water the Ca/Mg ratio in *Z. pedunculata* as well as in the *Ruppia* taxa increases whereas this ratio decreases in the water. In fig. 6 similar relationships are illustrated for the

K/Mg ratio in the plants and the water. The ratios found in the plants are much higher than in the water. The relationships in fig. 6C and 6D, however, look very similar. In this figure the chlorinity limits of the different community types are also indicated. The A7-A9 and A6 communities (dominant stands of *Z pedunculata*) were described by Van Vierssen (1982c). The relatively high K/Mg ratios in freshwater are caused by the relatively low Mg concentrations. The plants in the freshwater range have relatively high K/Mg ratios which are also caused by relatively low Mg concentrations

In fig. 7 similar relationships have been given for the K/Ca ratios in the plant and the water. The differences between the given relationships for the plants and the water are striking. Besides significantly higher ratios in the plants it is obvious that there are clear differences between the kind of relationships in fig. 7C and fig. 7D. The K/Ca ratios in *Z pedunculata* are relatively very high in the traject in which this macrophyte dominates compared with this ratio in *Potamogeton pusillus* and *Ruppia* taxa. This ratio is however relatively low in the same traject in fig. 7D. The relatively high K/Ca ratio in *Z pedunculata* in the slightly brackish waters is caused by a relatively high potassium content and a relatively low Ca content. The K/Ca ratios in the *Ruppia* plants are relatively low.

Discussion and conclusions

Because of the rather small size of the habitats and temporary character of many of them a rather diverse set of data was collected. This clearly had a negative influence on the comparison of all these data. A number of analyses of aquatic macrophytes are given by Harper & Daniel (1934), Bernatowitcz (1969), Boyd & Vickers (1971), Wali et al. (1972), Easly & Shirley (1974), Gommes & Muntali (1976), Kollman & Wali (1976), Shiber & Washburn (1978), Ho (1979) and Verhoeven (1979). When comparing the element constitution of the aquatic macrophytes from this present study with that of other aquatic macrophytes given in the literature quoted it is very difficult to indicate relevant and constant differences.

The authors mentioned determined element concentrations in whole plants most of the time. The distinction of different plant parts is essential, however, because the differences in element constitution can be considerable (Gerloff & Krombholz, 1966, Nichols & Keeney, 1976; Carpenter & Adams, 1977). What causes these differences is still under investigation. Much attention has been paid to the uptake and translocation of nitrogen and phosphorus. Twilley et al. (1977) discussed the uptake and translocation of phosphorus in *Nuphar luteum* (L.) Sibthorpe & Smith. This element was found to have a net acropetal transport largely influenced by the season. Certain amounts were excreted by roots and submerged leaves. Seadler & Alldridge (1977) studied the translocation of the same element in *Najas minor* All. These authors found an uptake by means of shoots and roots. Jeschka & Simonis (1965) found that phosphorus was taken up by the leaves of *Egeria densa* Planch. Bole &

Allen (1978) indicated an uptake of phosphorus by *Hydrilla verticillata* (L.f.) Royle and *Myriophyllum spicatum* L. from sediments in oligotrophic water. Welsh & Denny (1979) who studied the translocation of phosphorus in *Potamogeton pectinatus* and *P. crispus* found that this took place from and into the shoot. The uptake of phosphorus by duckweeds proved to be related to the $P\text{-}PO_4$ concentration of the ambient water, up to certain maximum levels (Sutton & Ornes, 1975). Nitrogen (in the NH_4 form) is taken up by the roots as well as by the shoots of *Myriophyllum spicatum* (Nichols & Keeney, 1976). This uptake depends on the $N\text{-}NH_4$ levels in the ambient water. When more $N\text{-}NH_4$ was present larger quantities were absorbed by the plants. According to these authors the uptake by the roots was sufficient for the plants. Toetz (1974) described the uptake of $N\text{-}NH_4$ by the roots of *Egeria densa* and *Ceratophyllum demersum.*

It is still very difficult to explain the element constitution of aquatic macrophytes in the field from laboratory experiments under controlled conditions. The plants that are collected are of a different age, the element concentrations in the water are not constant and the temperatures and light conditions fluctuate considerably. From the comparisons between the element constitution of *Z. pedunculata* and its accompanying macrophytes it follows that this species has characteristic nitrogen, phosphorus, magnesium and manganese concentrations in the aboveground plant parts. In the below-ground plant parts the potassium and sodium concentrations are characteristic. Potassium is the only element that was found in different concentrations in *Potamogeton pectinatus*, *P. pusillus* and *Z. pedunculata.* These macrophytes often grow together in the brackish communities dominated by *Z. pedunculata.* According to the relationships between the K/Ca, K/Mg ratios in the plants and the ambient water *Z. pedunculata* is especially characterized by its K/Ca ratio compared with the same ratio in *Potamogeton pusillus* (freshwater) and *Ruppia* species (mesohaline waters). These differences cannot be explained from the characteristics from the ambient water. As is also obvious from the cluster analysis of plants, potassium is very characteristic for *Z. pedunculata.* It cannot be excluded that the differences found between *Z. pedunculata*, *Potamogeton pectinatus* and *P. pusillus* (and *Ruppia* species) contribute to the niche differentiation between these aquatic macrophytes. Before drawing firm conclusions, however, the relationships between the growth of these macrophytes and different K/Ca, K/Mg ratios should be studied in monospecific stands. After that, similar experiments should be set up for mixed stands with these macrophytes. Such experiments might reveal whether the differences as found in this study between the macrophytes can be explained by clearly different physiological characteristics or not.

SOME NOTES ON THE DISTRIBUTION OF NUTRIENTS IN A *ZANNICHELLIA* DOMINATED ECOSYSTEM

Introduction

This part of the study deals with the distribution of a number of elements in the different parts of the ecosystem during one growing season. A brackish pool in Zeeuws-Vlaanderen (the Netherlands) with a monospecific vegetation of *Z pedunculata* was chosen as an example. The aim of this section is to indicate the quantitative importance of *Z pedunculata* with respect to the storage of elements compared with other parts of the system such as the sediments, the seston and the water.

Material and methods

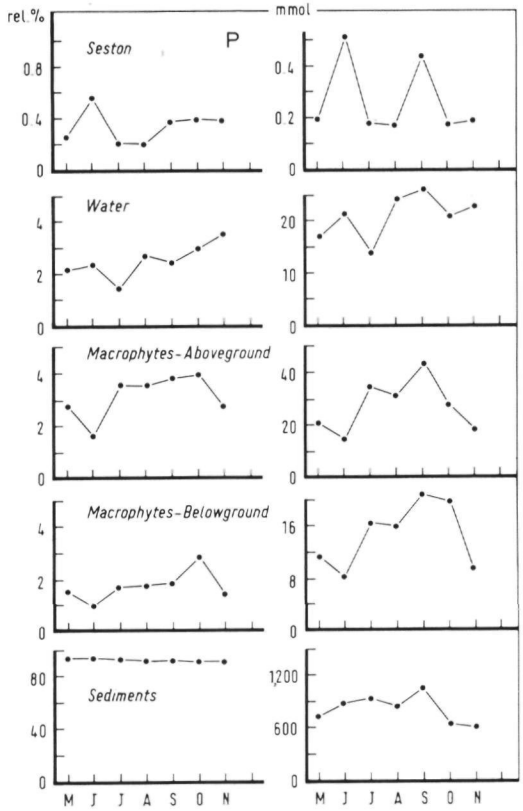
The pool in Zeeuws-Vlaanderen was sampled 7 times during 1979. Five different parts of the ecosystem were studied, viz. the water, the seston, the sediments, the above- and belowground parts of *Z pedunculata* The element concentrations in the water, the sediments and the plants were determined according to the methods described on p 165 The seston was treated as follows: its biomass was determined by filtering a given volume of water through a filter with a mesh-width of 3μm (Whatman GF/C glassfibre filter). This filter and a control blanco filter was dried at 105°C for 24 hours. After that, they were ashed (550°C, 4 hours) and the ash-free dry weight could be determined.

As a reference, chlorophyll-a was also determined in the samples (for methods see Moed, 1973; Moed & Hallegraeff, 1978, Roijackers, 1982). The digestion of the filters with and without seston was carried out in the same way as those of the plant material (see p. 165). The blanco filter was digested so that the amount of nutrients present in a filter could be subtracted from the total amount found.

For the calculation of the total amount of nutrients stored in the water layer, a mean water-level of 25 cm was considered. The top 5 cm sediment layer was considered to be the main reservoir of nutrients for the uptake of elements by the plants. In the next section the absolute and relative amounts (weight percentage) of nutrients stored in the different parts of the system are given for 1 m^2 with 25 cm standing water and a 5 cm deep sediment layer.

Results

In fig 10, 11, 12 and table IX the results are summarized. As is obvious from fig. 10, up tot 7% of the total amount of phosphorus present in the system is stored in the plant material. Of course, this quantity is relatively small compared with the total amount stored in the sediments. Up to 50% of the total amount of N, however, is temporarily stored in the plant material.



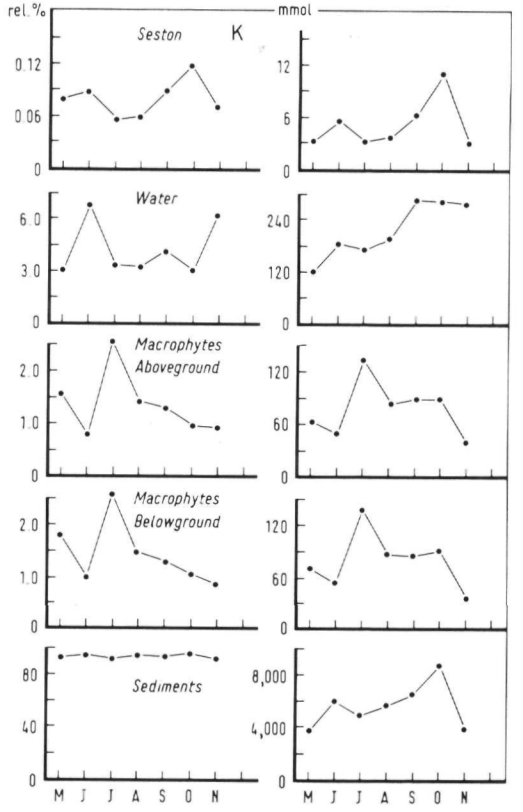


Fig. 10: Absolute (mmol) and relative (%) distribution of phosphorus over the different parts of the ecosystem (pool, Zeeuws-Vlaanderen).

Fig. 11: Absolute (mmol) and relative (%) distribution of potassium over the different parts of the ecosystem (pool, Zeeuws-Vlaanderen).

The seston material contains up to 6% of this element. These relatively large amounts in the water plants were found in September. The potassium content of *Z. pedunculata* proved to be relatively high but compared with the content of the other parts of the system the total amount in the plants is small. The sodium concentrations in the water are very high as it is brackish. The very low quantities of iron in the water and the plants are striking. It is obvious that only the nitrogen, phosphorus, manganese and potassium content of the waterplants are quantitatively of some importance.

Discussion and conclusions

It is obvious that the general survey as given in the previous section only offers a very approximate and static general image about the distribution of

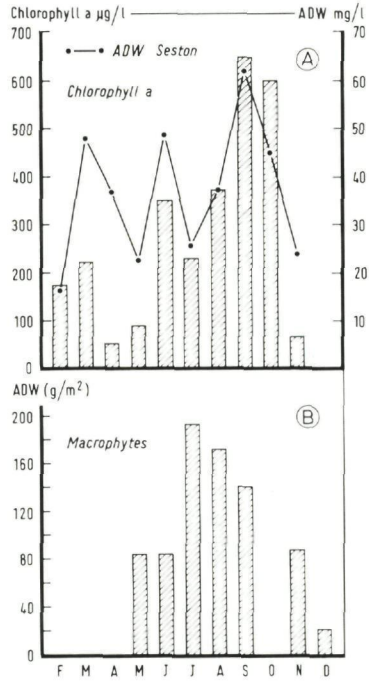


Fig. 12: A. Course of the chlorophyll-a concentration (μg/l) and the ash-free dry weight (ADW) of the seston during the growing season in a pool with *Z. pedunculata* (Zeeuws-Vlaanderen).
B. Course of the biomass of *Z. pedunculata* (ash-free dry weight in g/m^2) during the growing season in a pool in Zeeuws-Vlaanderen.

a number of elements over the different parts of the ecosystem. It is striking, however, that the plants store a considerable amount of nitrogen. The below-ground plant parts in particular showed a large storage of this element. The clear relationships between the K/Mg, K/Ca and Ca/Mg ratios in the plants and those in the water indicate that these elements are possibly mainly accumulated from the water.

EVALUATION OF THE RESULTS

When analysing the results it was quite clear that a regular sampling scheme was limited by the rather small size of the habitat. Further, the seasonal aspects of the vegetation stands resulted in a relatively low number of paired observations which was not beneficial for the processing of the data. However, a number of phenomena were obvious. The brackish waters in the Netherlands with communities dominated by *Z. pedunculata* have characteristic chlorinities and characteristic K/Ca, K/Mg and Ca/Mg ratios. There are

TABLE IX

Distribution of elements (absolute and percentual) over different parts of the ecosystem in a pool with a *Z. pedunculata* vegetation in Zeeuws-Vlaanderen (the Netherlands).

Element	Sediments Absolute					%					Water Absolute					%				
	Max	Min	Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min	Mean	S.D.	N	Max	Min	Mean	S.D.	N
N (mol)	546	168	419	137	7	88	52	66	13	7	73	36	53	15	5	14	6	9	3	5
Na (mol)	6,665	1,290	2,930	1,751	7	62	25	41	12	6	4,625	2,250	3,742	795	6	74	37	57	12	6
Ca (mol)	36,747	19,475	25,276	6,688	7	99	97	98	1	7	562	73	423	170	7	3	1	2	1	7
Mg (mol)	11,511	7,224	9,787	1,568	7	94	90	92	2	7	1,125	650	774	173	7	10	5	7	2	7
Fe (mol)	8,768	2,666	5,614	2,199	7	99	99	99	<1	4	1	1	1	1	4	<1	<1	<1	<1	4
Mn(mol)	831	39	252	261	7	99	90	96	3	7	17	<1	4	6	7	9	0	2	3	7

Element	Macrophytes *(Z. pedunculata)* Aboveground plant parts Absolute					%					Macrophytes *(Z. pedunculata)* Belowground plant parts Absolute					%				
N	78	30	63	17	6	19	4	11	5	6	173	44	106	48	6	30	9	17	7	6
Na	50	11	35	17	7	1	<1	1	<1	6	57	16	37	18	7	1	<1	1	<1	6
Ca	22	3	11	7	7	<1	<1	<1	<1	7	165	3	36	58	7	1	<1	<1	<1	7
Mg	20	6	12	5	7	<1	<1	<1	<1	7	26	8	17	8	7	<1	<1	<1	<1	7
Fe	5	1	2	1	7	<1	<1	<1	<1	4	1	<1	1	<1	4	<1	<1	<1	<1	4
Mn	2	1	1	1	7	5	<1	1	2	7	3	<1	1	1	7	1	<1	<1	<1	7

Element	Seston Absolute					%				
N	50	6	29	18	7	6	2	4	2	7
Na	54	22	38	13	7	1	<1	1	<1	6
Ca	11	2	4	3	7	<1	<1	<1	<1	7
Mg	13	2	5	4	7	<1	<1	<1	<1	7
Fe	3	1	2	1	7	<1	<1	<1	<1	4
Mn	1	<1	<1	<1	7	1	<1	<1	<1	7

significant differences between the element content of the aboveground and belowground plant parts. When comparing the most frequently occurring macrophytes in the communities viz. *Z pedunculata*, *Potamogeton pectinatus* and *P pusillus* it is striking that potassium occurs in significantly different concentrations in these macrophytes. Cluster analysis of plant parts of all macrophytes found together with *Zannichellia* (21 taxa) on the basis of complete sets of elements revealed that plant parts of species cluster. This means that the chemical characteristics of a species (the plant parts) are characteristic to such an extent that differences caused by different habitat characteristics are obviously of less importance.

Comparing *Z pedunculata*, *Ruppia maritima* and *Potamogeton pusillus* from neighbouring habitats it appeared that these species have very characteristic K/Ca, K/Mg and Ca/Mg ratios. Comparing these ratios with those in the ambient water it becomes obvious that *Z pedunculata* stores relatively high quantities of potassium where it occurs abundantly. It cannot be excluded that such special abilities lead to niche differentiation between plants. However, further experiments under controlled conditions are needed to be able to draw firmer conclusions.

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ON THE IDENTITY AND AUTECOLOGY OF *ZANNICHELLIA PELTATA* BERTOL. IN WESTERN EUROPE

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ABSTRACT

Van Vierssen, W. and van Wijk, R.J., 1982. On the identity and autecology of *Zannichellia peltata* Bertol. in western Europe. *Aquat Bot.*

To distinguish *Zannichellia peltata* Bertol. from other *Zannichellia* taxa in western Europe the general morphology and autecological characteristics of this taxon are presented. *Zannichellia peltata* has a chromosome number of $2n=12$. It was found that the seeds of this taxon germinate best at relatively low temperatures (about 12° C). After the seeds had been subjected to dry conditions, the optimum germination temperature appeared to be even lower (8° C). Under field conditions this results in a good germination in the autumn when temperatures fall and the dried up habitats are refilled with rainwater. The species shows a chlorinity tolerance not very different from that of *Z. palustris* L. and *Z. pedunculata* Rchb. Two varieties have been distinguished on the basis of plant morphological characteristics. *Z. peltata* var. *peltata* and *Z. peltata* var. *repens* var. nov. A diagnosis is presented for the latter.

INTRODUCTION

As was pointed out by van Vierssen (1982a, 1982c) three *Zannichellia* species can be distinguished in western Europe, viz. *Z. palustris* L., *Z. pedunculata* Rchb. and *Z. major* Boenn. In this paper a fourth species is distinguished. When Löve and Kjellqvist (1973) visited Spain, they found a *Zannichellia* taxon with $2n=12$ chromosomes. They identified their specimens as *Z. peltata* Bertol. and, according to them, this taxon is a species of southern or Mediterranean climates. The material used for their chromosome counts had been collected in a ditch near Cazorla (inland locality) in Spain.

Some years before, Reese (1957) had found the same chromosome number in *Zannichellia* material from the Algerian Sahara. Kozuharov and Kuzmanov (1964) recorded a *Zannichellia* taxon with this chromosome number in Bulgaria.

The present study reports the observations made by van Vierssen during a trip through Spain in May 1980. Additionally, the results of autecological

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experiments with this material are compared with the results obtained with the *Zannichellia* taxa from northern latitudes as published by Van Vierssen (1982 a, 1982b, 1982c).

CHROMOSOME NUMBER OF *ZANNICHELLIA* TAXA

Material and methods

Material of the various *Zannichellia* taxa from different latitudes was used for the chromosome counts. Seeds were available from the Camargue (kindly supplied by Prof. C. den Hartog) and Brittany (France), Greece (kindly supplied by H. Huijbregts), northern Europe (Finland, Denmark, The Netherlands) and Spain.

Root-tips from seedlings or plants which were cultured from seeds under laboratory conditions were collected. They were fixed with Navashin's solution. Microtome sections of 15 μm were made by the paraffin method and stained with Heidenhain's ironhaematoxilin and embedded in DePex. Chromosome counts were made in permanent slides by a light microscope at a magnification of 1000× or 2000×. Microphotographs were taken at a magnification of 1000×.

Results and discussion

The results of the chromosome counts are presented in Table I. Most of these counts were obtained from several metaphase configurations. In one instance no exact number could be obtained, and in this case the approximate

TABLE I

Chromosome numbers in *Zannichellia* taxa in western Europe

Taxon	Locality	Chromosome number ($2n$)
Zannichellia peltata var. *repens*	Loreto (Spain)	12
Zannichellia peltata var. *peltata*	Laguna de Medina (Spain)	12
Zannichellia peltata var. *peltata*	Villafranco (Spain)	12
Zannichellia peltata var. *peltata*	Granada (Spain)	12, 36
Zannichellia peltata var. *repens*	Camargue (France)	12
Zannichellia palustris ssp. *repens*	Tvärminne (Finland)	24
Zannichellia palustris ssp. *repens*	Lith (The Netherlands)	24
Zannichellia palustris ssp. *repens*	Ringköbing Fjord (Denmark)	36
Zannichellia palustris ssp. *palustris*	Mühlbach (W. Germany)	24
Zannichellia palustris ssp. *palustris*	Alexandria (Greece)	24
Zannichellia pedunculata	Camargue (France)	ca. 36
Zannichellia pedunculata	Groningen (The Netherlands)	36
Zannichellia pedunculata	Zeeuws-Vlaanderen (The Netherlands)	36
Zannichellia pedunculata	Ile de Batz (France)	36

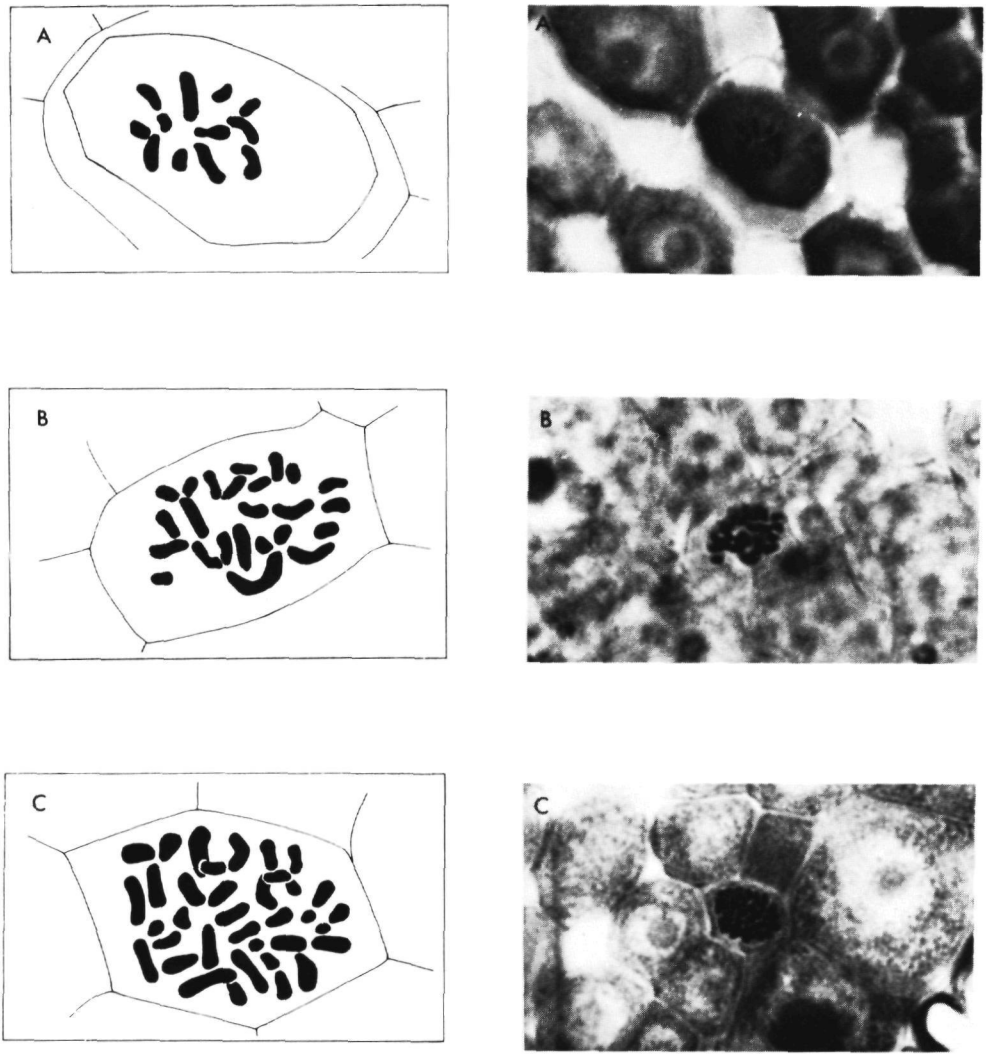


Fig. 1. Drawings and photographs of chromosome configurations. A: *Zannichellia peltata* (Laguna de Medina, Spain), $2n=12$; B: *Zannichellia palustris* (Alexandria, Greece), $2n=24$; C: *Zannichellia pedunculata* (Ile de Batz, France), $2n=36$.

number has been given. In contrast to the chromosome numbers which were found in the material from northern Europe ($2n=24$ and $2n=36$), most of the plants from the southern part of western Europe (southern Spain) appeared to have $2n=12$ chromosomes. In the Camargue, one population with this number was found.

Figure 1 shows photographs and drawings of the chromosome configurations as found in the di-, tetra- and hexaploid *Zannichellia* taxa. From the counts, it is concluded that the basic chromosome number is 6, as Reese (1967) had already postulated.

Fig. 2. General appearance of *Zannichellia peltata* Bertol.

In Table I two aberrant chromosome numbers from *Zannichellia* material are obvious; $2n=36$ in *Z. palustris* from the Ringkøbing Fjord (Denmark) and $2n=36$ in *Z. peltata* from Granada (Spain). The *Z. palustris* material from the Ringkøbing Fjord was collected in a mixed population of this taxon with *Z. pedunculata*.

In the *Zannichellia* material collected near Granada the $2n=36$ number was exceptional. Most of the material contained $2n=12$ chromosomes. The *Zannichellia* plants with $2n=36$ chromosomes were also identified as *Z. peltata*, however, because of the morphological characteristics (Fig. 2). It is suggested that because of the evolutionary development of different polyploid taxa from the diploid and tetraploid taxa, such polyploid specimens may be expected to occur occasionally.

MORPHOLOGY OF *Z. PELTATA*

General vegetative morphology

Within *Z. peltata* two different growth-forms occur. These growth-forms are genetically determined because after cultivation from seeds under controlled conditions the morphological characteristics of these forms persist.

Seedlings of the one growth-form immediately produced caulescent shoots and later on horizontal runners. Seedlings of the other growth-form produced first horizontal runners which could cover a large area, and later small upright shoots; the number of horizontal runners in this form is much higher than in the first mentioned form. The two growth-forms are recognized as varieties, var. *peltata* and var. *repens* var. nov., respectively.

Morphology of the inflorescence

The male flower of *Z. peltata* is the most characteristic. The plants with the $2n=12$ chromosomes all have full-grown stamens of at least 3 cm in length, in most instances even 5—7 cm. This is considerably longer than the stamens of the other *Zannichellia* taxa, which are never longer than 2 cm. The female inflorescence comprises two carpels, seldom one or three. The stigma is peltate with a rather irregular-shaped outline (Fig. 3). We never observed a clearly denticulate stigma as described by Bertoloni (1854). When the water-level falls, the plants often partly emerge above the water-surface. In that case the stigmas of this taxon show their very characteristic solidity. They keep their original shape for a relatively long time, in contrast to the stigmas of the other *Zannichellia* species. It seems as if air is retained within the tissue structures which gives these stigmas their bright appearance under such conditions.

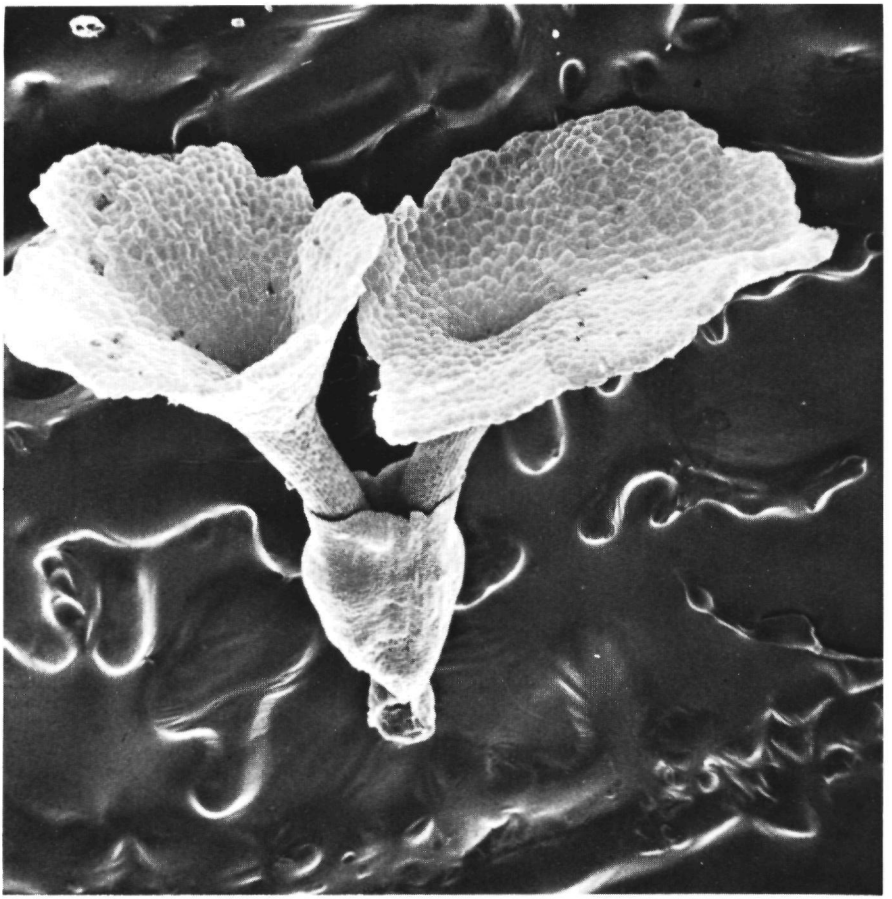


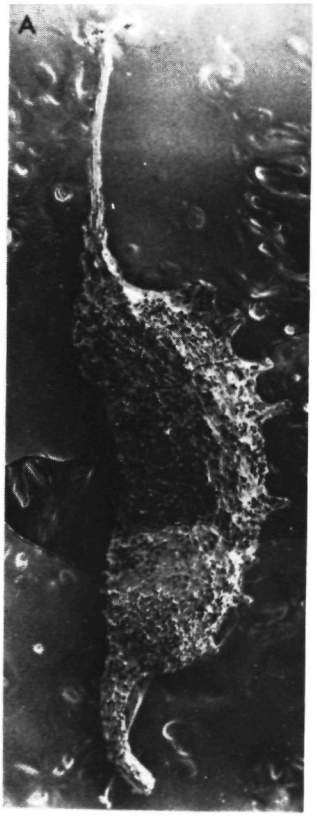
Fig. 3. Inflorescence of *Zannichellia peltata* showing peltate stigmata.

Fruit and seed morphology

The rostrum length divided by the fruit length appeared to be a very useful ratio to distinguish between *Z. palustris* and *Z. pedunculata* (van Vierssen, 1982a). The rostrum of *Z. peltata* seeds is longer than half the fruit length. Therefore this characteristic is unsuitable for distinguishing between *Z. peltata* and *Z. pedunculata.* In fact, the seeds of *Z. peltata* resemble those of *Z. pedunculata.*

Zannichellia peltata has two types of seeds which can be distinguished by their length. They both have the same rostrum/fruit length ratio, however. The larger seeds (with an average length of 2.7 mm) were collected in three localities; the Camargue (France), Loreto and Granada (both in Spain). The

Fig. 4. Seeds of, A: *Zannichellia peltata* var. *repens* var. nov. (Camargue, France); B: *Z. peltata* var. *peltata* (Villafranco del Guadalquivir, Spain); C: *Z. peltata* var. *peltata* (Laguna de Medina, Spain); D: *Z. peltata* var. *repens* (Loreto, Spain).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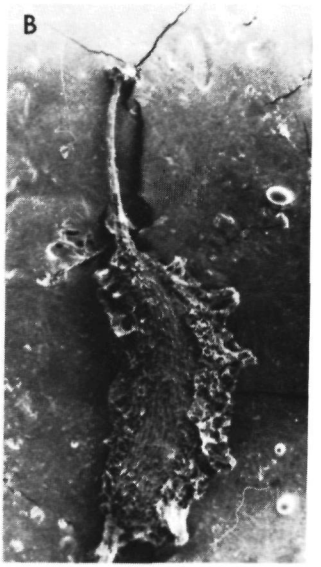
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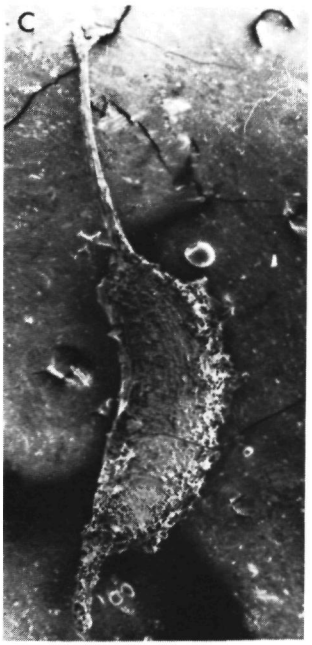
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D

plants cultivated from these seeds were identified as *Z. peltata* var. *repens*. The smaller seeds (with an average length of 2.3 mm) were collected in three localities in Spain: Laguna de Medina, Laguna del Taraje and Villafranco del Guadalquivir. These seeds belonged to var. *peltata*. Fig. 4 shows the seeds of these two varieties.

Discussion and conclusions.

According to Löve and Kjellqvist (1973), their *Zannichellia* material with $2n=12$ chromosomes was *Z. peltata*. Bertoloni (1854) presented a *Zannichellia* taxon with a characteristic long stamen. As no other *Zannichellia* taxon with such a long stamen has ever been found in western Europe, it is reasonable to suppose that Bertolóni's material is identical with the *Zannichellia* material with $2n=12$ chromosomes. From a photograph of the type specimen it was obvious that it had relatively small seeds. Willkomm and Lange (1870) mentioned three *Zannichellia* taxa of which *Z. macrostemon* Gay is considered as identical with *Z. peltata*. In Ascherson and Graebner (1907) this taxon has been described as having long stamens. They quote Willkomm and Lange (1870) as their source, although the long stamens are not mentioned there.

The *Zannichellia* material with the relatively large seeds and the creeping growth-form collected by us is described here as a new variety of *Z. peltata* Bertol.

Zannichellia peltata var. repens var. nov.

Differt a *Z. peltata:* primo surculis numerosis relative brevibus; secundo seminum magnitudin patum ampliore (plus minusve 2.7 mm); tertio plantula initio stolones horizontales efferente. Locus typicus: Pool near Loreto, Spain.

Differs from *Z. peltata* by: (1) many relatively short shoots; (2) the slightly larger size of the seeds (average 2.7 mm); and (3) by the fact that initially the germling produces horizontal runners.

The type specimen of this variety has been deposited in the Rijksherbarium at Leiden, The Netherlands.

AUTECOLOGICAL EXPERIMENTS WITH *Z. PELTATA*

Material and methods

Seeds collected in May in the Laguna de Medina and a small pond near Loreto have been used for germination experiments. The experiments were carried out under long-day conditions (17 μE m^{-2} s^{-1}, 16 h light, 8 h dark) and in the dark. At each temperature (8, 12, 16, 20, 24°C) and chlorinity (0, 2, 4, 6, 8, 10, 12‰), 25 seeds were used. The germination of the seeds is given by means of the germination percentage (GP) and the harmonic mean germination day index (HMGD; van Vierssen, 1982a). The growth ex-

periments with *Z. peltata* were carried out in glass aquaria. In these experiments the influence of different clorinities (0, 2, 4, 6, 8‰) on the development of the plants and certain morphological characteristics (shoot-length, share of the rhizome in the total biomass) was studied. Ten seedlings of *Z. peltata* and *Z. pedunculata* (as a reference) were planted in separate com-

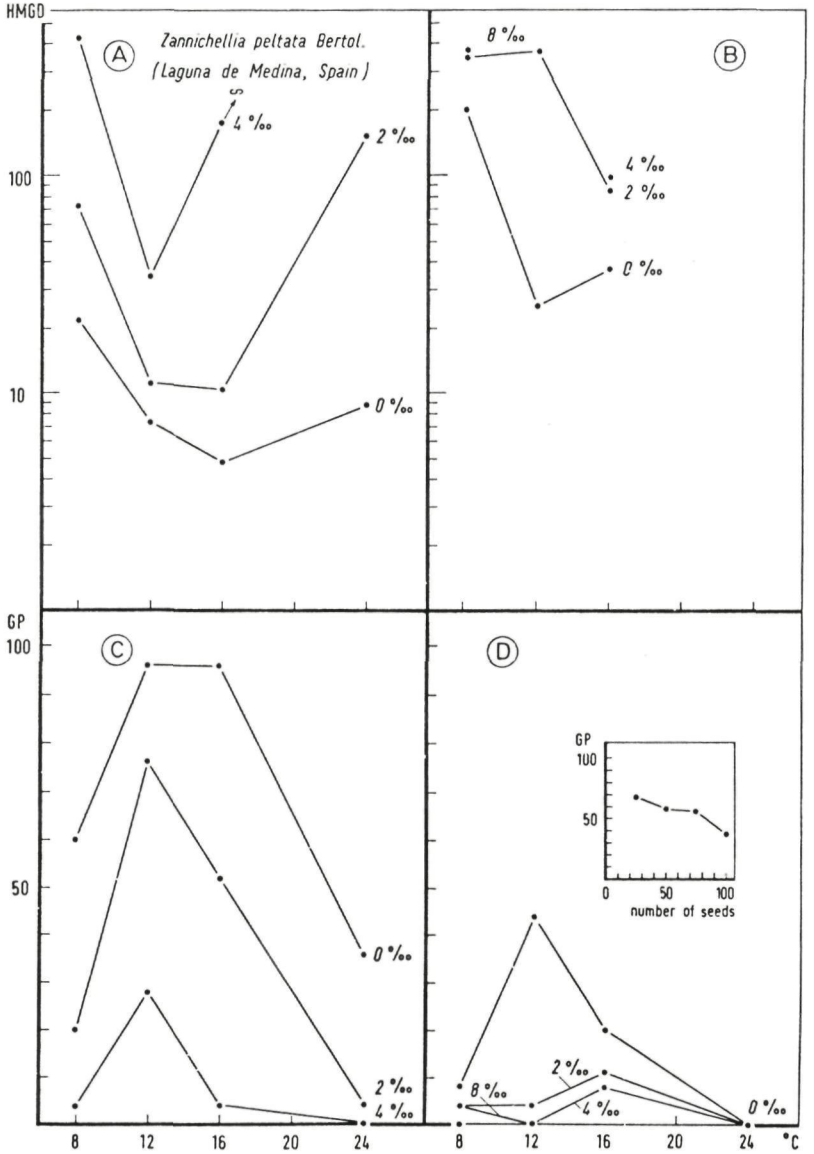
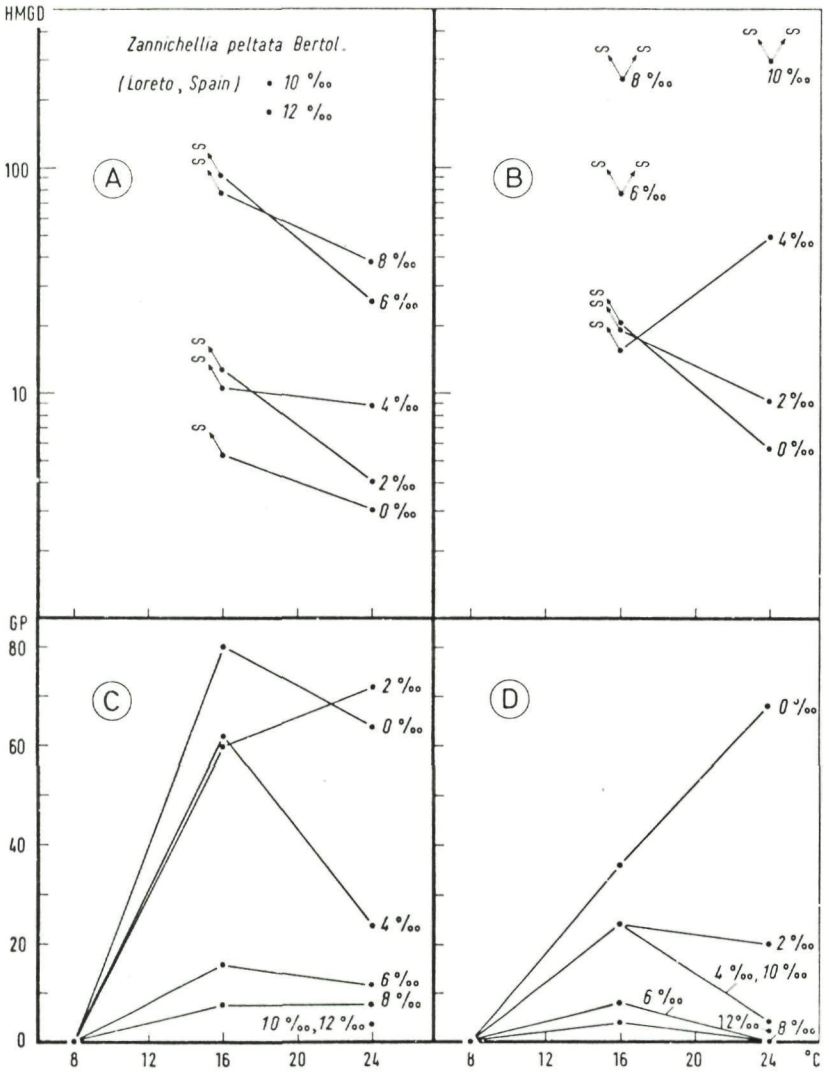


Fig. 5. Germination of seeds of *Zannichellia peltata* var. *peltata* (Laguna de Medina) in relation to chlorinity and temperature expressed as HMGD (A,B) and Germination Percentage (C,D) under long day (A,C) and dark (B,D) conditions. Inset: Correlation between number of seeds used in a petri dish and the germination percentage.

partments which were flushed with the same medium. Coverage estimates were made by rectangular projection of the plant parts on the bottom. The length of the longest shoot was taken as a measure for the rate of vertical development. From the moment this particular shoot reached the water-surface this length was no longer measured.

Seed germination in relation to chlorinity, temperature and desiccation

The results of these experiments have been summarized in Fig. 5 for *Z. peltata* var. *peltata* and in Fig. 6 for *Z. peltata* var. *repens*. The inset in Fig. 5D shows that there is a negative correlation between the number of seeds and the germination percentage. Therefore, the same number of seeds was used



in all experiments. Seeds of *Z. peltata* var. *peltata* germinated only at 0, 2 and 4 ‰ Cl^- under long-day conditions, but not at higher chlorinities. At higher chlorinities no germination at all occurred. The optimum germination temperature changes from 16° C at 0‰ and 2‰ Cl^- to 12° C at 4‰ Cl^- (Fig. 5A). Germination of more than 50% occurs at relatively low chlorinities and temperatures. Germination in the dark is clearly slower (larger HMGD), and germination percentages are all below 50%. The experiments with seeds of *Z. peltata* var. *repens* from Loreto show slightly different results. The germination under light conditions shows an optimum at 24° C (HMGD), but at 16° C according to the germination percentages. In the dark germination occurs at a somewhat lower rate (Fig. 6).

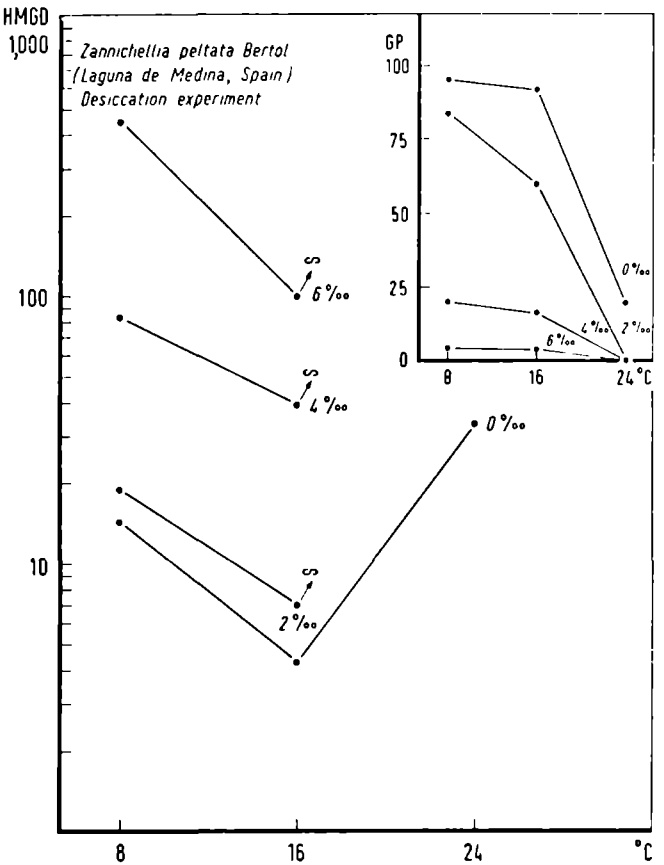


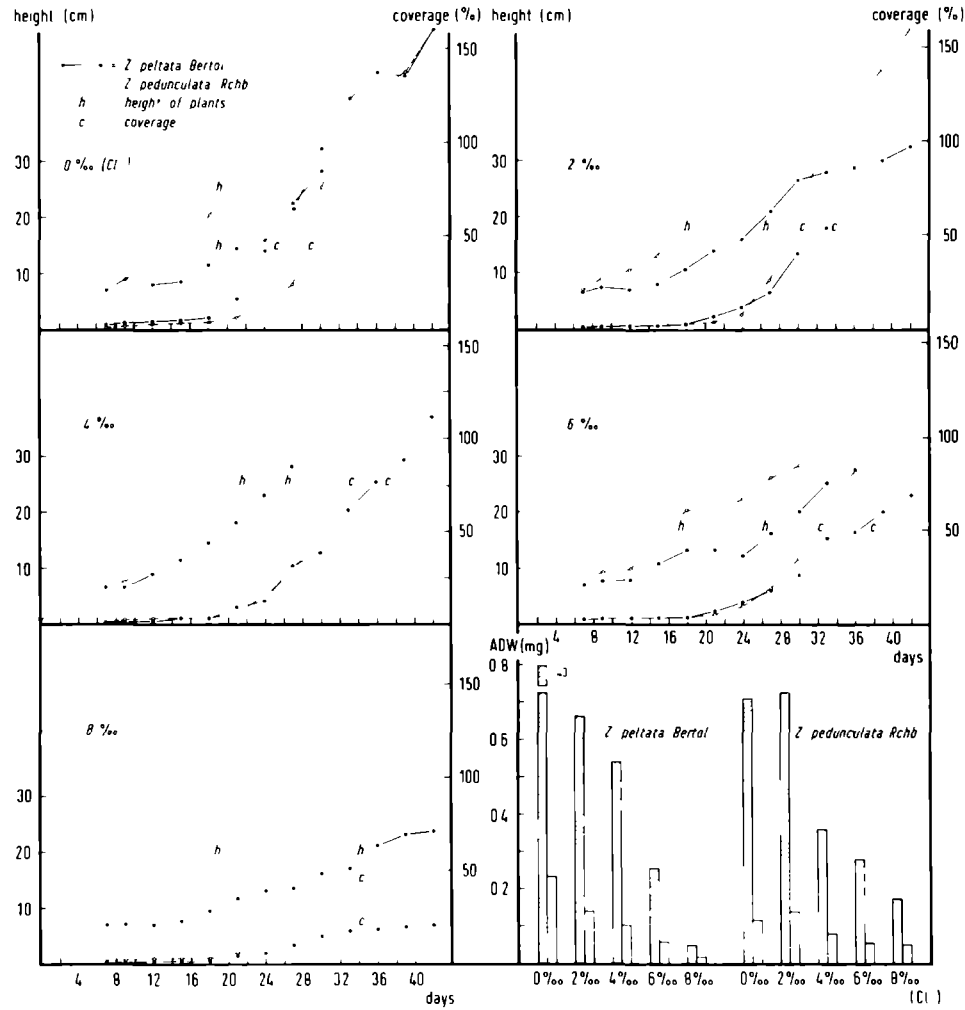
Fig. 7 Germinations of seeds of *Zannichellia peltata* var. *peltata* (Laguna de Medina) in relation to chlorinity and temperature expressed as HMGD and Germination Percentage after desiccation (long day conditions).

Fig. 6. Germination of seeds of *Zannichellia peltata* var. *repens* (Loreto) in relation to chlorinity and temperature expressed as HMGD (A,B) and G.P. (C,D) under long day (A,C) and dark (B,D) conditions.

Some desiccation experiments were carried out with *Z. peltata* var. *peltata* seeds from the Laguna de Medina. After a period of dry conditions (2.8% water was left in the substrate) these seeds were subjected to the same experimental conditions as were used in the germination experiments above. As is illustrated in Fig. 7 the HMGD figures are not very much affected by desiccation in contrast to the germination percentages. The optimum germination temperature is now 8° C instead of 12° C before desiccation. When 50% germination is considered as a minimum percentage for a good germination, it can be stated that generally chlorinities above 2—3 ‰ are unsuitable.

Growth and development of Z. peltata *in relation to chlorinity*

In Fig. 8 the results of the coverage estimates and the shoot-length measurements during a period of 43 days are given. During the first ten days there



are hardly any differences between *Z. peltata* and *Z. pedunculata*. After this period, however, *Z. peltata* var. *repens* remained rather small, producing relatively numerous small shoots, whereas *Z. pedunculata* produced a relatively low number of long shoots. After the shoots reached the water-surface no further length measurements were made. However, the plants produced more biomass. Therefore the cover percentages still increased. From this figure it appears that the vertical growth (= height) of *Z. pedunculata* was faster than that of *Z. peltata*, whereas the horizontal development (= initial coverage) of *Z. peltata* was faster.

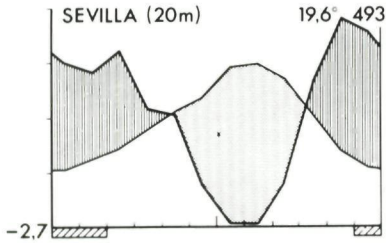
In Fig. 8 the biomass (expressed as ash-free dry weight) of the two *Zannichellia* stands at the end of the experiment is also given. The biomass has been differentiated into rhizome and shoot material. It is obvious that the biomass of *Z. peltata* steadily decreased in relation to the increasing chlorinity. At 0 and 2‰ Cl^- the *Z. pedunculata* stand produced about the same biomass. At higher chlorinities this species also steadily produced less. The share of the rhizome parts in the total biomass of the species is about the same for both species. Calculating the ratio between the biomass of one specimen and the rhizome of the same specimen, this ratio ranges between 6.1 and 2.8 for *Z. peltata* and between 6.1 and 3.3. for *Z. pedunculata*.

It appears that *Z. peltata* is somewhat less chlorinity tolerant than *Z. pedunculata*. At 8‰ Cl^- all plants of *Z. peltata* were in a bad condition. This chlorinity is considered as the absolute tolerance limit for *Z. peltata* when grown under stable chlorinity conditions.

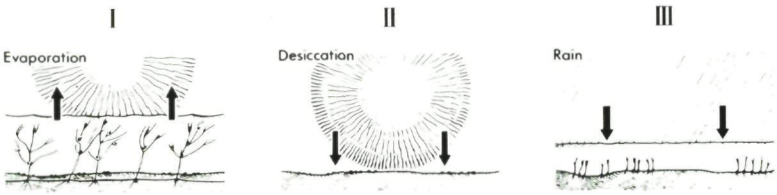
LIFE-CYCLE OF *Z. PELTATA* UNDER FIELD CONDITIONS

It is obvious that in the summer period, droughts frequently occur in southern Europe. When visiting the localities near Villafanco del Guadalquivir in May, in the shallow marshes from which seeds of *Z. peltata* were collected the sediments were completely dry. Figure 9 is a schematic representation of such a dried-out habitat with *Z. peltata*. The climate diagram (Walter and Lieth, 1967) illustrates the general climatic conditions. Arid conditions occur during a period of four months. How do the *Zannichellia* plants manage to survive these unfavourable conditions? In May the seeds do not germinate because of the relatively high chlorinity of the water (strong evaporation) and the high water temperatures. These conditions inhibit germination, as has been found in the experiments. Desiccation is tolerated by the seeds and it lowers the already low optimum germination temperatures. When the autumn rains refill the habitats in November and December the low temperatures are favourable for germination and a rapid development of a *Zannichellia* stand. The maximum biomass of such a stand is to be expected in winter.

Fig. 8 Height of plants, coverage and biomass of *Zannichellia peltata* and *Z. pedunculata* in relation to chlorinity (‰). The ash-free dry weights (ADW) of the above-ground plant parts are given by means of striated bars.



LIFE-CYCLE OF
***Zannichellia peltata* Bertol.**
(Villafranco, SPAIN)



	I	II	III
Season:	May	June - October	November-April
Water T:	> 20° C	Desiccated	± 12°C
Phenomena:	– Deposition of seeds – Relatively high chlorinity – Desiccating habitat – No germination	– Desiccated habitat – Seeds not damaged	– Refilling of habitat by rain – Slow dissolving of salts – Germination of seeds
Cause:	– Relatively high chlorinity (> 3 à 4 ‰) inhibits germination – Relatively high temperature inhibits germination because of the low optimum germination temperature	– Drought resistant seeds	– Good germination because optimum temperature has been lowered due to desiccation – Low chlorinity

Fig. 9. Life-cycle of *Zannichellia peltata* under field conditions (Villafranco del Guadalquivir).

Comparing the life-strategies of *Z. peltata* with those of the other *Zannichellia* species in western Europe some general trends are obvious. *Zannichellia major* is a perennial with a very low seed production and is completely adapted to permanent habitats. The number of temporary habitats increases from north to south because of the changes in the climatic conditions (increasing temperature, desiccation due to evaporation). Species that occur in such habitats show gradually lower optimum germination temperatures (*Z. palustris*, 24° C; *Z. pedunculata*, 20° C and *Z. peltata*, 12° C). Environmental factors such as desiccation and chlorinity stress (which increase in importance going south) lower these temperatures even more. This phenomenon is clearly related to the optimalisation of the development of

plant species during the most favourable period of the year. Thus in northern Europe the species behave as summer annuals, while in southern Europe they are winter annuals.

The chlorinity tolerances of *Z. palustris*, *Z. pedunculata* and *Z. peltata* do not differ very much. Habitat differentiation is obviously not only achieved by chlorinity tolerance of the plants, but mainly by means of a different germination ecology.

COMMUNITY STRUCTURE AND SPECIES COMPOSITION OF THE PHYTOCOENOSES WITH *Z. PELTATA*

The species composition of the phytocoenoses with *Z. peltata* is not very different from those with *Z. pedunculata* in other parts of western Europe *Z. peltata* var. *repens* has been found in a pond near Loreto in a belt along the edge of the water (40 cm wide belt). This belt consisted of *Z. peltata* plants with numerous small shoots and rather robust horizontal runners. In this pool *Potamogeton pectinatus* L. occurred in the deeper parts (more than 30 cm deep). The stands of these two species within this habitat were almost completely separated (for relevé see Table II).

Near Granada a streamlet was found with a monospecific vegetation of *Z. peltata* var. *repens* at the margin. Because of decreasing rainfall in May this vegetation slowly dried out.

In a number of coastal habitats *Z. peltata* var. *peltata* was found in slightly brackish waters. In the Laguna del Taraje (a dune lake in the Coto de Doñana), *Z. peltata* var. *peltata* occurred together with *Potamogeton pectinatus*

TABLE II

Species composition of communities with *Zannichellia peltata* in Spain*

Locality**	1	2	3	4	5
Depth (cm):	28	25	20	30	50
Chlorinity (‰):	0.018	0.053	0.62	3.017	2.84
Date (1980):	4-5	5-5	8-5	8-5	9-5
Substrate:	Sand	Silt	Silt	Silt	Silt
Ruppia maritima cf var. *longipes* Hagström	—	—	—	—	1
Zannichellia peltata var. *repens* var. nov.	4	2a	—	—	—
Zannichellia peltata Bertol. var. *peltata*	—	—	2	3	4
Potamogeton pectinatus L.	—	5	1	1	1
Ranunculus spec.	—	—	1	—	—
Myriophyllum spicatum L.	—	—	+	—	—
Chara hispida L.	—	—	—	1	—

*Relevés according to the scale of Barkman et al. (1964)

** (1) running water near Granada (Spain); (2) small pool near Loreto, Spain; (3) Laguna del Taraje, Coto de Doñana, Spain; (4) Laguna del Taraje, Coto de Doñana, Spain; (5) Laguna de Medina, Spain.

(dominant), *Ranunculus* spec. and *Chara hispida* L. In the Laguna de Medina, *Z. peltata* var. *peltata* was found together with *Ruppia maritima* L. (probably var. *longipes* Hagstrom) (see also Van Vierssen et al., 1981) and *Potamogeton pectinatus* at a chlorinity of 2.84‰. Near Villafranco del Guadalquivir seeds of *Z. peltata* var. *peltata* were found in bottom sediments. The identity of the material was confirmed after culturing of the plants in Nijmegen (The Netherlands). From the mass of dried up plant material covering the ground, it was obvious that a rather luxuriant *Z peltata* var. *peltata* vegetation must have been present during the winter months.

Too few localities with *Z. peltata* have been studied to draw firm conclusions with respect to the most usual species combinations. There are however obvious similarities between these communities and those with *Z. pedunculata* in other western European localities.

GENERAL CONCLUSIONS

It appears from this study that *Z. peltata* is a well-defined taxon. Two varieties have been distinguished; *Z. peltata* var *peltata* and *Z peltata* var. *repens* var. nov. The distinction is based on different growth-forms and the morphology of seeds. The distinction of *Z. peltata* from other western European *Zannichellia* species is based on morphological, karyological and autecological characteristics. The germination of seeds obviously plays an important role in the ecology of *Z. peltata*. Compared with *Z palustris* and *Z. pedunculata* the seeds of this taxon have the lowest optimum germination temperature. This is a clear adaption to the climatic conditions in southern Europe. *Zannichellia peltata* is an annual which completes its life-cycle in the winter The chlorinity tolerance of the species does not differ very much from that of *Z. palustris* and *Z. pedunculata*. The habitat differentiation of these *Zannichellia* species in western Europe is considered to be mainly caused by this different germination ecology. The species composition of the communities with *Z. peltata* is rather similar to those with *Z. pedunculata*.

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De oecologie van gemeenschappen gedomineerd door *Zannichellia* soorten in West Europa

In deze studie, die bestaat uit een viertal artikelen, worden een aantal aspecten besproken betreffende de oecologie van gemeenschappen gedomineerd door *Zannichellia* soorten in West Europa. Het geslacht *Zannichellia* bestaat uit ondergedoken waterplanten met fijne, lijnvormige bladeren. Het geslacht komt over de gehele aarde verspreid voor in zoet en brak water.

Deze studie behandelt in het eerste artikel de morfologie van het Europese *Zannichellia* materiaal zoals dat verzameld is in Finland, Denemarken, Nederland, Duitsland, Frankrijk en Spanje. Door middel van experimenten in het laboratorium met zaden en planten van de *Zannichellia* soorten die op grond van morfologische en karyologische verschillen onderscheiden zijn, is gepoogd deze differentiatie te ondersteunen.

In een tweede artikel zijn de veldwaarnemingen verwerkt in relatie tot de resultaten uit de experimenten uit het eerste artikel. Tevens bevat dit gedeelte een classificatie op basis van de soortensamenstelling van de fauna en de waterplanten en de hoeveelheid materiaal die er door geproduceerd wordt.

Deel drie behandelt de opslag en verdeling van een aantal elementen in en over de waterplanten en een aantal oecosysteem compartimenten. Tevens wordt ingegaan op de verschillen in gehaltes zoals deze tussen de verschillende soorten macrophyten werden aangetroffen.

Deel vier beschrijft tenslotte de oecologie van een *Zannichellia* soort die tegen het einde van het onderzoek in Zuid Europa is aangetroffen. Een uitgebreide beschrijving van dit materiaal complementeert de monografie over de Westeuropese *Zannichellia* soorten.

In de nu volgende uitgebreide samenvatting van de studie zijn de resultaten uit het vierde artikel ondergebracht bij de resultaten van de andere drie delen, teneinde een samenhangend beeld te verschaffen.

I. De morfologie en autoecologie van de verschillende *Zannichellia* soorten

De morfologische verschillen tussen de verschillende *Zannichellia* soorten kunnen als volgt worden samengevat. *Z peltata* Bertol. wordt gekenmerkt door een zeer lange meeldraad (tot 7 cm) in tegenstelling tot de meeldraadlengte bij de andere soorten, die maximaal 2 cm bedraagt. *Z major* Boenn. heeft relatief grote, volgroeide vruchten (> 3 mm), terwijl deze in de twee resterende soorten kleiner zijn (< 3 mm). *Z palustris* L. en *Z pedunculata* Rchb. tenslotte zijn duidelijk te onderscheiden met behulp van de ratio bestaande uit de lengte van het rostrum gedeeld door de lengte van de vrucht. Komt deze ratio boven 0.5 uit, dan behoort het materiaal tot *Z pedunculata*, er beneden, dan is er sprake van *Z palustris* Ook karyologisch zijn er duidelijke verschillen aanwezig. *Z. peltata* wordt gekenmerkt door 2n = 12

chromosomen, *Z palustris* door 2n = 24, en *Z pedunculata* door 2n = 36 chromosomen. *Z major* bevat volgens literatuurgegevens 2n = 32 chromosomen.

Uit de kiemexperimenten kunnen de volgende samenvattende conclusies getrokken worden. Zaden van *Z palustris* kiemen alleen goed na een koude behandeling (4 °C) van enkele maanden. De beste kieming vindt plaats bij 24 °C in zoet water. Boven 4 ‰ Cl′ vindt geen kieming meer plaats. Zaden van *Z pedunculata* daarentegen kiemen goed onder lange dag condities zonder een koude behandeling. In het donker vindt geen kieming plaats De optimum temperatuur is 24 °C in zoet water. Na een koude periode van enkele maanden vindt wel kieming in het donker plaats en is bovendien de optimum temperatuur verlaagd. Uitdroging en hoge temperaturen (32 °C) brengen geen schade toe aan de kiemkracht. De zouttolerantie van deze zaden bedraagt maximaal 12 ‰ Cl′.

De zaden van *Z peltata* hebben ook geen koude inductie nodig om te kiemen. Opmerkelijk is dat de optimum kiemingstemperatuur slechts 12 °C bedraagt. Na uitdroging is deze zelfs verlaagd tot 8 °C. *Z major* zaden kiemen goed, doch spelen geen rol van betekenis in de levenscyclus van deze soort.

De planten van *Z palustris*, *Z pedunculata* en *Z peltata* vertonen ongeveer dezelfde zouttolerantie; 8 ‰ Cl′. *Z major* werd niet getest, doch komt onder natuurlijke omstandigheden tot 11 ‰ Cl′ voor. Wisselende chloride gehaltes worden het beste verdragen door *Z pedunculata* in vergelijking met *Z palustris* Wanneer deze twee taxa in mengcultures samen gekweekt worden onder deze omstandigheden, blijkt duidelijk dat competitie tussen deze soorten zulke veranderingen in de groeivorm van de planten veroorzaakt dat *Z pedunculata* duidelijk gaat domineren. Dit feit is terug te voeren op de produktie van lange scheuten door *Z pedunculata*, en een duidelijke afname van het in de monocultuur duidelijk grotere aantal korte scheuten bij *Z palustris* Deze afname wordt zowel door het fluctuerende chloride gehalte alsook door de competitie met *Z pedunculata* veroorzaakt.

II. Verspreiding, synoecologie en produktiviteitsaspecten

Z palustris komt voornamelijk in de noordelijke en continentale streken van West Europa voor. Dit feit kan verklaard worden uit de benodigde koude periode voor de zaden om het volgende seizoen weer te kunnen kiemen. *Z pedunculata* heeft zijn optimale verspreiding duidelijk zuidelijker, van Denemarken tot Zuid Frankrijk. De zaden van deze soort zijn droogteresistent. De onder experimentele omstandigheden vastgestelde kiemingsvoorwaarden komen goed overeen met de veldsituatie.

Het zwaartepunt van de verspreiding van *Z peltata* ligt in Zuid Frankrijk en het Iberisch schiereiland. Uitdroging is een dominerend verschijnsel op deze breedtes in de zomermaanden. De gevonden zeer lage optimum kiemingstemperatuur is verantwoordelijk voor kieming in de herfst. Dit heeft tot gevolg dat *Z peltata* een kenmerkend winterannual karakter vertoont, met

een zaadproduktie die optimaal is voordat in het voorjaar de milieus weer uitdrogen. De geconstateerde verschillen in groeivorm tussen *Z pedunculata* en *Z palustris* verklaren ook voor een gedeelte het gescheiden voorkomen in delen van Noord Europa.

Z major is in het bezochte gedeelte van West Europa beperkt tot het noordelijke deel (Oostzee, Botnische Golf). De soort is duidelijk overjarig en heeft een erg lage zaadproduktie. Daardoor komt de soort uitsluitend in permanente wateren voor.

Bij het beschrijven van de gemeenschappen op grond van de floristische samenstelling is onderscheid gemaakt tussen brakke wateren en stilstaande en stromende wateren. In het brakke water van West Europa zijn een elftal gemeenschappen onderscheiden waarin *Zannichellia* soorten domineren. Belangrijke begeleidende soorten zijn *Zostera marina* L., *Potamogeton filiformis* Pers., *Ruppia maritima* L. var. *maritima*, *Potamogeton pectinatus* L., *Potamogeton pusillus* L., *Ranunculus baudotii* Godr., *Chara canescens* Desv. et Lois. en *Chara aspera* Dethardng ex Willdenow. In Noord Europa zijn deze gemeenschappen permanent van karakter, terwijl zuidelijker de factor uitdroging geleidelijk gaat overheersen. Het aantal soorten neemt hierdoor ook af.

In stilstaande zoete wateren zijn een viertal gemeenschappen onderscheiden met een onderling vaak erg afwijkend karakter, maar vooral ook zeer afwijkend van de gemeenschappen in brak water. *Z palustris* is meestal niet dominant aanwezig, doch vaak wel kenmerkend voor de gemeenschap. Belangrijke begeleidende soorten zijn *Potamogeton pectinatus*, *Potamogeton pusillus*, *Potamogeton crispus* L., *Nymphoides peltata* (Gmel.) O. Kuntze, *Nuphar lutea* (L.) Sm. en *Potamogeton perfoliatus* L. In stromend water, een habitat type slechts enkele malen bestudeerd, zijn twee gemeenschappen onderscheiden met *Z. palustris* Belangrijke begeleidende soorten zijn *Ranunculus fluitans* Lamk., *Potamogeton perfoliatus*, *Callitriche* sp. en *Groenlandia densa* (L.) Fourr.

De classificatie op basis van de fauna vond alleen plaats in het brakke water van West Europa. Dit heeft geleid tot het onderscheiden van een zestal gemeenschappen. In Noord Europa zijn de brakwater organismen en de euryhaliene marlene organismen ruim vertegenwoordigd, met soorten behorende tot de Crustacea en Mollusca. Het totaal aantal macrofauna soorten bedraagt maximaal 35. In de wat meer zuidelijk gelegen wateren (Nederland) is een duidelijke tweedeling aan te geven die berust op het permanente of tijdelijke karakter van de habitats. In de meer permanente milieus zijn maximaal zo'n 70 soorten aanwezig (Insecta, Mollusca) waarvan de groep der aquatische kevers het soortenrijkst is. In de meer tijdelijke milieus zijn wat minder soorten te vinden (maximaal 30), met een duidelijke dominantie van de Insecta (voornamelijk aquatische keversoorten). In Zuid Frankrijk (Camargue) is de soortensamenstelling in de tijdelijke milieus zeer verschillend. Het soortenaantal is vrij laag (24) en bestaat voornamelijk uit aquatische stadia van landinsecten.

De kwantitatieve aspecten van de gemeenschappen zijn eveneens onder-

zocht. Wat betreft het aantal organismen (en de biomassa ervan) dat aanwezig is nemen *Macoma baltica* (L.) en *Nereis diversicolor* (O.F. Müll.) in Noord Europa een belangrijke plaats in (totaal aantal organismen per m^2 tussen 4700 en 15800, biomassa per m^2 tussen 1,1 en 19,5 g). In Nederland zijn de Chironomidae larven, *Lymnaea peregra* (Müller) en *Planorbis planorbis* (L.) erg belangrijk (totaal aantal organismen per m^2 tussen 900 en 28800, biomassa per m^2 tussen 1,6 en 22,9 g). In Zuid Europa (Camargue) zijn erg weinig organismen aanwezig (totaal aantal organismen per m^2 tussen 700 en 1200, biomassa per m^2 tussen 0,15 en 0,42 g).

Het aantal individuen in de door *Zannichellia* gedomineerde systemen is relatief groot in vergelijking tot de aantallen in zoet water. Vergeleken met de mesohaliene gemeenschappen gedomineerd door *Ruppia* soorten zijn de aantallen echter relatief laag. Het is opvallend dat in de *Ruppia* gemeenschappen enkele soorten domineren, terwijl dit in de *Zannichellia* gemeenschappen minder het geval is (echter vaker dan in zoetwater gemeenschappen).

De diversiteitsindex van Shannon-Weaver benadert dan ook de waarden bekend voor zoetwater systemen (voor de aantallen organismen tussen 0,61 en 2,37, voor de biomassa's tussen 0,86 en 2,71). Ze zijn echter gemiddeld beduidend hoger dan in de brakkere gemeenschappen met *Ruppia* soorten.

De gevonden maximale macrophyten biomassa's van de verschillende gemeenschappen (met vaak een aantal verschillende soorten macrophyten) varieerden tussen 70 g en 300 g per m^2. Deze getallen liggen in dezelfde orde van grootte als de biomassa's die in gemeenschappen met zoetwater macrophyten gevonden worden. De mariene zeegras gemeenschappen produceren echter beduidend meer plantenmateriaal. De conclusie is gerechtvaardigd dat de structurele relatie tussen de fauna en de vegetatie in de *Zannichellia* gedomineerde gemeenschappen marginaal is. Het plantemateriaal vervult een tamelijk neutrale rol in de totstandkoming van een bepaalde fauna-samenstelling.

III. Chemische samenstelling van de waterplanten en een aantal oecosysteem-componenten in relatie tot omgevingsfactoren

De chemische samenstelling van de macrophyten (Na, K, Mg, Mn, Ca, Fe, N, P) in een groot aantal door *Zannichellia pedunculata* gedomineerde gemeenschappen is bestudeerd in relatie tot dezelfde elementgehaltes in een aantal systeemcomponenten zoals de bodem en het water. Het blijkt dat bij clustering van de planteonderdelen (bovengronds, ondergronds) op basis van de complete set van elementgehaltes de onderdelen van één soort de grootste overeenkomst vertonen. Er bestaan duidelijke verschillen tussen het gehalte van een element in de ondergrondse en bovengrondse plantedelen. Op basis van vergelijkingen tussen frequent samen voorkomende macrophyten zoals *Zannichellia pedunculata*, *Potamogeton pectinatus* en *Potamogeton pusillus* zijn overeenkomsten en verschillen tussen deze macrophyten vastgelegd.

Kalium neemt een duidelijk centrale plaats in bij de clustering van de macrophyten.

Na bestudering van de K/Ca, K/Mg en Ca/Mg ratio's in zowel een aantal waterplanten als ook in het water van de monsterpunten blijkt dat deze ratio's zeer karakteristiek zijn voor deze macrophyten. Bij een vergelijking tussen monsterpunten met respectievelijk *Ruppia* soorten, *Zannichellia pedunculata* en *Potamogeton pusillus* blijkt dat er karakteristieke verschillen in deze ratio's aanwezig zijn. Bij de bestudering van de opslag van nutrienten in verschillende compartimenten van een poel met *Zannichellia pedunculata* blijkt dat maximaal 50% van de totale hoeveelheid stikstof die aanwezig is in een sectie van 1 m^2 met een diepte van 25 cm en een 5 cm dikke bodemlaag opgeslagen is in de waterplanten. In vergelijking met de opslag door waterplanten van andere elementen (vaak minder dan 1%) is dit erg veel.

Wilhelmus van Vierssen werd op 7 december 1951 te Eindhoven geboren. In Nijmegen werd in 1969 het diploma HBS-b behaald, waarna in september van datzelfde jaar de studie Biologie aan de Katholieke Universiteit werd begonnen. Op 6 maart 1973 werd het kandidaatsexamen B3 succesvol afgelegd. In het kader van de doctoraalstudie werd in 1973 onderzoek verricht op de Boschplaat (Terschelling) naar de verspreiding en oecologie van *Scirpus rufus* (Huds.) Schrad. Ter completering van dit hoofdvak geobotanie werd in 1975 een literatuurstudie verricht betreffende een classificatiesysteem voor de Nederlandse floraelementen. In 1974 werd onderzoek verricht naar het renine-angiotensine systeem bij de Afrikaanse klauwpad *(Xenopus laevis)* op de afdeling Medische Biologie van de Medische Faculteit te Nijmegen (bijvak Dierfysiologie). Als laatste onderdeel van de studie werd onderzoek verricht in *Ruppia* gemeenschappen op Texel (bijvak Aquatische Oecologie). Op 6 april 1976 werd het doctoraalexamen Biologie met lof afgelegd.
Met behulp van een promotiebeurs van het Ministerie van Onderwijs en Wetenschappen kon bij de afdeling Aquatische Oecologie het promotie-onderzoek in door *Zannichellia* gedomineerde gemeenschappen worden aangevangen. Per 1 januari 1977 volgde een aanstelling als wetenschappelijk medewerker aan de Katholieke Universiteit op basis van een door het Ministerie van Volksgezondheid en Milieuhygiene aan het project toegekende financiële steun. Vanaf 1 november 1977 volgde een aanstelling aan dezelfde Universiteit vanwege de toekenning van een universitaire onderzoeksplaats.
In maart 1976 werd een studiereis gemaakt samen met Dr. J.T.A. Verhoeven naar Corsica. In het kader van het promotieonderzoek werd in juni-juli 1978 het "Institut fur Seenforschung und Fischereiwesen" te Reichenau (West Duitsland) bezocht. In juni 1978 volgde een studiereis door Denemarken en noord Duitsland. Tevens werd in dat jaar een bezoek gebracht aan het "Tvarminne Zoological Station" te Tvarminne (Finland). In mei 1980 werden Frankrijk (Station Biologique de Tour du Valat, Camargue) en Spanje (Universiteit van Sevilla) bezocht in het kader van het promotieonderzoek.
Op 24 januari 1981 werd een voordracht gehouden te Brussel in het kader van het "International Colloqium on Aquatic Vascular Plants" met als titel: "Reproductive Strategies of *Zannichellia* taxa in western Europe".
Sinds 1 januari 1981 is hij in dienst van de Landbouwhogeschool te Wageningen als wetenschappelijk medewerker bij de Vakgroep Natuurbeheer.

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STELLINGEN

I

Ondanks het feit dat in Zuid-Europa de door *Zannichellia* gedomineerde oecosystemen zijn opgebouwd uit zoutminnende plantesoorten en gereguleerd worden door het zoutgehalte, kunnen deze oecosystemen op basis van hun faunistische soortensamenstelling als zoetwatersystemen opgevat worden.

Dit proefschrift

II

Op grond van de overlevingsstrategieën van de soorten die participeren in de brakwatervegetaties van de Carmargue, kunnen deze vegetaties beschouwd worden als intermediair tussen de typisch mediterrane en atlantische brakwatervegetaties.

III

De door macrofyten gedomineerde brakwateroecosystemen in Nederland vormen één der meest bedreigde oecosysteemtypes.

IV

Bij het karakteriseren van gemeenschappen door middel van produktiecijfers dient meer aandacht besteed te worden aan de concurrentie tussen soorten en de invloed hiervan op de produktiemogelijkheden van deze soorten.

V

Het beheer van door waterplanten gedomineerde oecosystemen dient door fundamenteel oecologisch onderzoek ondersteund te worden.

VI

Het onderwijs in de plantensociologie vormt een essentieel onderdeel van de opleiding tot plantenoecoloog.

VII

Vanwege de beperkte oppervlakte van Nederland, en de schaal waarop populatie-dynamische processen plaatsvinden, dienen de beperkingen ten aanzien van dienstreizen naar het buitenland, in het kader van oecologisch onderzoek, zo beperkt mogelijk te zijn.

VIII

Gezien de maatschappelijke consequenties die politici trekken uit de uitkomsten van oecologisch en milieuhygienisch onderzoek, kan de bezigheid van de betrokken wetenschappers het beste omschreven worden als bezigheidstherapie.

IX

Het verwijt van sommige politici dat het zgn. 'doemdenken' leidt tot een 'self-fulfilling prophecy' wordt veelal ingegeven door eigenbelang.

X

Een volk krijgt de jeugd die het verdient.

XI

Het journaal voor doven en slechthorenden is niet om aan te zien.

W. van Vierssen